AN INTEGRATIVE SYSTEMATIC REVISION OF THE CHLORODIELLINAE NG & HOLTHUIS, 2007 (CRUSTACEA: DECAPODA: BRACHYURA: XANTHIDAE)

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The xanthid subfamily Chlorodiellinae is one of the most widespread and common coral reef crab taxa in the Indo-West Pacific, with 5 genera and 30 species. Members of the subfamily often dominate rocky shore and coral rubble habitats in terms of biomass and likely play a major role in coral reef food webs. Despite their ubiquity and importance, the taxonomy of Chlorodiellinae was in serious need of revision. The systematics of the Chlorodiellinae is revised at the subfamily, genus, and species level. A molecular phylogeny of Xanthidae, incorporating previously published sequence data, is presented, with more complete sampling of the subfamily than previous studies, clarifying the evolutionary relationships of Chlorodiellinae. Based on a four-marker (COXI, 12S, 16S, H3) phylogeny and additional morphological evidence, five genera (*Ratha*, *Liocarpilodes*, *Tweedieia*, *Sulcodius*, and *Vellodius*) are removed from the Chlorodiellinae. Two new genera, *Soliella* and *Luniella*, are erected; after polyphyletic relationships in *Pilodius* were revealed. These new taxa are described in the context of both morphology and molecular phylogenetics. The restricted subfamily now comprises *Chlorodiella*, *Cyclodius*, *Pilodius*, *Soliella*, and *Luniella*. A new genus, *Ratha*, is described for the sole Western Atlantic nominal species, *Chlorodiella longimana*, and is removed from the subfamily. Last, the species-level classification of Chlorodiellinae is revised using gonopod morphology, as well as gene trees and combined molecular analyses. The utility of gonopod morphology for species delineation is discussed in light of molecular and geographic distribution data.

DISCLAIMER

In accordance with Article 8.3 of the Fourth Edition of the International Code for Zoological Nomenclature (henceforth referred to as the Code), this work is hereby declared as not having been issued, or intended for publication in its present form, for public or permanent scientific record. New names or statements pertaining to nomenclatural acts within this work are to be treated as not published within the meaning of the Code.

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CHAPTER 1.
GENERAL INTRODUCTION

Recent evidence suggests that 53 to 70 percent of the oceans' species have yet to be discovered (Appeltans *et al.* 2012). Although new initiatives and technology (e.g., Census of Marine Life; National Science Foundation Partners for Enhancing Expertise in Taxonomy; decapod, bivalve and cnidarian A Tree Of Life projects; improved integrative taxonomy and molecular phylogenetics methods) are generating an overwhelming amount of marine biodiversity and evolutionary data, a lack of baseline taxonomic research is limiting our ability to understand these data. Meanwhile, current rates of extinction have risen to ca. 1000 times the background rate of extinction (Pimm *et al*. 2014), and our oceans are being increasingly degraded via acidification, warming, overfishing, pollution, and development (Polidoro *et al*. 2011, McCauley *et al*. 2015). Given the current biodiversity crisis and bewildering amount of undiscovered marine taxa, revisionary taxonomy is urgently important.

Integrative Taxonomy and Delineating Species

Integrative taxonomy is the combination of genetically independent data from multiple fields of study to inform discovery, delineation, identification, and classification of organisms (Will *et al*. 2005, Dayrat 2005, Padial *et al*. 2010, Schlick-Steiner *et al*. 2010). Sources of data in fields such as population genetics, ecology, anatomy and physiology, acoustics, and behaviour are being increasingly used to improve rigor in species delineation. Congruence between different data sources provides evidence that the evolutionary history behind speciation has been discovered (Hillis 1987). Beyond traditional morphological taxonomy, molecular genetics has been relied upon heavily. DNA barcoding has been the focus of much of the relatively recent integrative taxonomy literature, with over 1000 publications on the subject (Goldstein & DeSalle 2010). For example, DNA barcoding has promised to accelerate the slow grind of species discovery and description (Hebert & Gregory 2005)—a nice thought, but controversial (Wheeler, 2004; Will and Rubinoff, 2004; Ebach and Holdredge, 2005; Will et al., 2005). Despite the promise, there is often conflict between molecular and morphological data.

Conflicts in delineation arise due to many methodological and evolutionary, or intrinsic, reasons (Evans & Paulay 2012). Indistinguishable morphology (sibling or convergent species), insufficient sampling, and intraspecific variation (sexual dimorphism, polymorphism and phenotypic plasticity) sometimes make sole use of morphology difficult or ineffective (Mayr 1942, 1963, Knowlton 1993, Moore & Willmer 1997). Molecular data is also sensitive to sampling and intraspecific variation. These problems are further exacerbated by different rates of evolution among genes (e.g., different gene trees versus species trees) (Funk & Omland 2003), low sample size may obscure speciation boundaries, and there are numerous challenges to analyzing sequence data (e.g., NUMTs, barcode gaps, and different phylogenetic inference methods).

Complicating matters further, species delineation hinges on the proper application of a species concept. However, given the more than 20 species concepts available and immense body of literature on the subject, choosing one concept and defending it can be bewildering (Mayden 1997, Hey J.

2006). Even so, the theoretical framework provided by choosing a species concept is necessary, as the use of different concepts may result in different number of species recognized (Laamanen *et al*. 2003, Agapow *et al*. 2004, Tan *et al*. 2008, Tan *et al*. 2009, Schwentner *et al*. 2011). Helpfully, many of the numerous species concepts fit into the five outlined in Wheeler and Meier (2000): the Biological Species Concept (BSC), the Hennigian Species Concept (HSC), the two Phylogenetic Species Concepts (PSC), and the Evolutionary Species Concept (ESC).

In the present study, the HSC and BSC are applied following the arguments of Meier and Willmann (2000). The Hennigian and Biological species concepts stress reproductive isolation as the mechanism resulting in speciation and determining species boundaries (Meier & Willmann 2000, Mayr 2000). They differ mainly in how ancestral species are treated. The present study only explicitly deals with the delineation and description of extant crabs, so the application of either concept would produce the same results. Mishler and Theriot's (2000) PSC defines species based on monophyly and whether a clade is "worthy of formal recognition", or "the least inclusive taxon recognized in a formal phylogenetic classification". According to the authors, formal recognition relies on support for monophyly and "importance in biological processes operating" on the "species". However, this definition is inherently arbitrary, as the determination of a "species" clade would be affected by character choice (e.g., genes used in molecular analysis), resolution (affected by character choice and analytical method), taxon selection, or whatever one might consider "worthy of formal recognition". On the other hand, Wheeler & Platnick's (2000) PSC defines species as the "smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states". A key reason for rejecting this concept in the present study is that populations evolve unique combinations of characters states, and thus, in light of intraspecific variation, determining whether an aggregation is a population versus a species is arbitrary and hinges on which character states one chooses to apply. The ESC states that a species "maintains its identity from other (species) through time and over space and that has its own independent evolutionary fate and historical tendencies". Wiley and Mayden (2000) insist that hybridization resulting in viable offspring may occur between species, as long as these events are "outliers". The problem here is that judgment on how much hybridization between species is allowed for these events to be considered outliers is arbitrary, and so the ESC is rejected. Furthermore, Laamanen *et al*. (2003) pointed out that reproductive isolation between populations satisfies the criteria that species have different "evolutionary fates" and "historical tendencies", so application of the ESC in this case would not produce different results from that of HSC.

Despite the theoretical strength of delimiting species based on reproductive isolation, inferring reproductive isolation can be practically difficult. However, differences in genital morphology between closely related species is common across many animal phyla (Eberhard 1985). The mechanism causing differentiation is a longstanding question (Hosken & Stockley 2003), one that has never been addressed in brachyura. However, pre and postcopulatory barriers to reproduction attributed to genitalic diversity have been documented in many arthropod groups (Eberhard 1985). Furthermore, xanthid crabs have male gonopods that are markedly variable between species (Guinot 1968a, Serène 1984). Here, chlorodielline crabs are delineated with special emphasis on the integration of molecular data and male gonopod morphology.

History of Xanthidae

The pantropical Xanthidae MacLeay, 1838, is one of the most diverse families of brachyuran crabs, with over 600 described species (Ng *et al*. 2008) that generally inhabit pantropical rocky substrates and coral reefs. The family's taxonomy has undergone substantial change due to the initial reliance on analogous morphological characters such as the "xanthoid carapace shape" (Balss 1957; Glaessner 1969; Serène 1962, 1971, 1984; Serène and Nguyen 1960; Guinot 1967a,b,c, 1968a,b,c, 1969a,b,c,d, 1971,1976, 1977a,b, 1978, 1979; Serène & Umali 1972; Serène & Vadon 1981; Martin & Davis 2001; Stevcic 2005, Ng *et al*. 2008) . Recent phylogenetic and taxonomic studies have cast serious doubt on the utility of many characters previously used for taxonomic delimitation and have identified suites of potential new characters (Ng *et al*. 2008, Lai *et al.* 2011, Lasley *et al*. 2013, Thoma *et al*. 2013). Furthermore, these studies have indicated that many, if not most, of the Xanthidae's subfamilies are in serious need of taxonomic revision—Chlorodiellinae being one.

With 50 described species in eight genera, chlorodielline crabs are widely distributed throughout the tropical and subtropical Indian and Pacific oceans, with one western Atlantic representative (Ng *et al.* 2008, Mendoza & Manuel-Santos 2012, Lasley *et al.* 2013). Members of the subfamily are abundant on rocky seashores, within live coral, and, most notably, in coral rubble. They often dominate coral reef cryptofauna in terms of biomass (pers. obs., Peyrot-Clausade 1977, Peyrot-Clausade 1979), and are especially common in microhabitats that have been recently targeted in large-scale biodiversity surveys—e.g., dead *Pocillopora* heads, and Autonomous Reef Monitoring Structures (ARMS) (Plaisance *et al.* 2011). Furthermore, chlorodielline crabs likely play a major ecological role in reef food webs, as a recent study carried out on five species of reef associated fishes in French Polynesia indicated that 37 percent of the crustaceans found in gut contents were chlorodielline crabs (extrapolated from Leray *et al.* 2012).

Delimiting the Chlorodiellinae Ng & Holthuis, 2007, is difficult due to tenuous inter- and intrafamilial relationships. The subfamily has traditionally been characterized by spoon-tipped chelae; a non-projecting front; a broad, transversely ovate carapace; and a dactylo-propodal locking mechanism on the walking legs (*sensu* Serène 1984). Many of these characters, however, are present in genera of other subfamilies (e.g., *Cymo*: Cymoinae, *Leptodius*: Xanthinae, *Etisus*: Etisinae, *Kraussia*: Kraussiinae, and *Garthiella*: Garthiellinae) (Ng *et al*. 2008, Mendoza & Manuel-Santos 2012). Furthermore, Chlorodiellinae's closest relatives—namely Etisinae—are polyphyletic (e.g., see Lai *et al*. 2011) and defined by morphological characters of doubtful homology, making generic assignment based on common ancestry difficult (Ng *et al*. 2008, Felder & Thoma 2010, Lai *et al*. 2011).

Dana (1851) described the subfamily "Chlorodinae" in four sentences, and included genera from several xanthid subfamilies, and even the genus *Daira* (now in the Dairidae). Subsequent authors split and reorganized the subfamily with varying results. Most notably, Serène (1984) gave a concise historical review of "Chlorodiinae" and limited the taxon to five genera (*Chlorodiella* Rathbun, 1897; *Cyclodius* Dana, 1851; *Pilodius* Dana, 1851; *Liocarpilodes* Klunzinger, 1913; and *Tweedieia* Ward, 1934). *Chlorodiella* became the type genus, but only after considerable taxonomic confusion.

The first mention of the genus *Clorodius* Desmarest, 1823, the initial type genus of Chlorodiinae Dana, 1851, was made in a footnote of A. G. Desmarest's work, "Malacostracés" (1823). There, Desmarest stated that

Fabricius had erected the name *Clorodius* for *Cancer dentatus*, which, he said, has denticulate, spoon-tipped chelae (Desmarest 1823: 228). However, as mentioned by Rathbun (1897a: 156), there is no species named "*Cancer dentatus* Fabricius." Later, H. Milne Edwards (1834: 399–401) described *Chlorodius* H. Milne Edwards, 1834 (a misspelling of "*Clorodius*") as being close to *Xantho* Leach, 1814 but with a narrower carapace and spoon-tipped chelae. He also placed several species that share a suite of morphological characteristics (e.g., spoon-tipped chelae and a similarly-shaped, broad, transversely-ovate carapace) in *Chlorodius* while designating *Chlorodius niger* (Forskål, 1775) as the type species. Rathbun (1897a) later changed *Chlorodius* to *Chlorodiella*, citing that *Chlorodius* is a junior synonym of *Atelecyclus* Leach, 1814. All of the species originally placed in *Chlorodius* by H. Milne Edwards (1834) have subsequently been assigned to other xanthid genera (e.g., *Chlorodiella* Rathbun, 1897a; *Pilodius* Dana, 1851; *Leptodius* A. Milne-Edwards, 1863; and *Cyclodius* Dana, 1851). Ng and Holthuis (2007) reviewed the confused nomenclatural history of the group that resulted in the necessary replacement of the subfamilial name from Chlorodinae to Chlorodiellinae Ng & Holthuis, 2007.

Cyclodius Dana, 1851 (type species: *Cyclodius ornatus* Dana 1852, subsequent designation by Rathbun, 1922), also has a colorful taxonomic history. Despite Dana (1851: 126) having described *Cyclodius* 12 years before A. Milne-Edward's (1863) description of *Phymodius* (type species: *Chlorodius ungulatus* H. Milne Edwards, 1834), Gordon (1934: 32) inexplicably stated in a footnote that *Cyclodius* probably ought to be a junior synonym of *Phymodius*, not the other way around. Forest & Guinot (1961: 104) confirmed Gordon's suggestion and the name *Phymodius* was in use until Davie (2002: 520) resurrected the name *Cyclodius*. Ng *et al*. (2008) also used the name *Cyclodius*, citing Rathbun's (1922) submission of 99 generic names to the International Commission for Zoological Nomenclature (Opinion 73, Direction 37). Hence, the name *Phymodius* is considered a subjective synonym of *Cyclodius*. *Pilodius*, Dana, 1851 (type species: *Chlorodopsis melanochirus* A. Milne Edwards, 1873), has remained in use since its description, although A. Milne-Edwards' (1873) described the junior synonym, *Chlorodopsis* (type species: *Chlorodopsis melanochirus* A Milne Edwards, 1873) (see *Pilodius* remarks for explanation of synonymy).

Three monotypic genera were added to Serène's (1984) assemblage: *Sulcodius* Clark & Ng, 1999; *Vellodius* Ng & Yang, 1998; and *Garthiella* Titgen, 1986. *Garthiella* was eventually assigned to its own monotypic subfamily, Garthiellinae Mendoza & Manuel-Santos 2012. The genera *Sulcodius* and *Vellodius* were thoroughly compared to *Cyclodius*, *Pilodius*, and *Chlorodiella* in their original descriptions (Ng & Yang 1998, Clark & Ng 1999). However, only cursory attention was given to *Liocarpilodes* and *Tweedieia*—both mentioned only briefly and without figures. The focus on *Cyclodius*, *Pilodius*, and *Chlorodiella* to the exclusion of *Liocarpilodes* and *Tweedieia* is indicative of the evolutionary history of the group, which has recently been supported in part by molecular phylogenetic studies (Lai *et al*. 2011, Lasley *et al*. 2013).

In addition to nomenclatural issues, several chlorodielline species- and genus-level delimitation problems have arisen in the literature. Much of the confusion appears to be due to the high degree of convergence between species and variation within species. For example, three major revisionary works that focused on *Chlorodiella* indicated difficulties in differentiating species of the genus (Forest & Guinot 1961, Serène 1984, Dai & Yang 1984). Much the confusion stems from the *Chlorodiella's* glabrous carapace, which is devoid of features often used for species delimitation. In short, *Chlorodiella* species all look superficially alike. Furthermore, the genus *Pilodius* was relatively recently revised by Clark & Galil (1993). The study provided illustrations and diagnoses of each species which, when compared, reveal morphological groupings with shared characters that conflict with the diagnosis of the genus—e.g., the morphology of the basal antennal segment (see Chapter 3). Beyond these divisions, the key provided is inadequate for identification, as it includes features that are variable within species or hard to appreciate (e.g., the division of carapace region 2M and the presence of conical granules on the anterolateral margins). *Cyclodius* has not been subject to a comprehensive revision, and *Liocarpilodes* appears to be a conglomeration of unrelated genera, based on carapace and G1 morphology (Chapter 5). In addition, there are many questionable species, some of which have been bouncing in and out of synonymy (e.g., *Pilodius philippinesis*) (Chapter 6).

In view of these problems, the following are general objectives for the present work:

1. To delimit the Chlorodiellinae from other xanthid subfamilies using molecular phylogenetics and morphology,
2. To taxonomically redefine the Chlorodiellinae,
3. To elucidate the nomenclature and taxonomy of chlorodielline genera based on molecular data and morphology,
4. To revise the species-level taxonomy of the Chlorodiellinae,
5. To provide keys, diagnoses, and diagnostic figures for all chlorodielline taxa.

CHAPTER 2.
MATERIAL AND METHODS

Material Examined

Material examined in this report is deposited at the following institutions: Florida Museum of Natural History, Gainesville, Florida, USA (UF); University of Louisiana at Lafayette Zoological Collection, Lafayette, Louisiana, USA (ULLZ); National Museum of Natural History, Washington DC, USA (USNM); Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC); Queensland Museum, Brisbane, Australia (QM); Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China (only last three digits of catalog numbers recorded) (IOCAS); and Senckenberg Museum, Frankfurt am Main, Germany (SMF). The identity of certain species is difficult to determine without adult male specimens or COXI sequences. When identity of a specimen is uncertain, the record is preceded by a "(?)". If all specimens from a locality cannot be confidently determined, the locality is preceded by "(?)". Measurements, presented in millimeters (mm), are of the carapace width and length, respectively. Conventions for carapace region designations (e.g., 1F, 1M, etc.) follow Dana (1852). The abbreviations G1 and G2 refer to the male first and second pleopods, respectively, and ovig. = ovigerous. GPS coordinates are reported as recorded on specimen vials, including decimal degrees; centroid; and degrees, minutes and seconds. An asterisk after the catalog number indicates the specimen has been used in the molecular analyses.

Definition of Terms

General terminology follows Serène (1984) and Ng *et al*. (2008) (Figs 1, 2). Carapace regions follow Dana (1851) (Fig. 3). Authors differ on which teeth are included as part of the anterolateral margin. Here, Dana (1851) is followed. The anterolateral teeth are counted starting laterally after the outer supraorbital tooth (fig. 3).

Two historical features have been discussed frequently in literature and are important for understanding chlorodielline taxonomy: the basal antennal segment and tip of the ambulatory leg dactylus. The expansion of the anterolateral angle of the basal antennal segment is an important character for distinguishing genera (Fig. 10). In some genera (e.g., *Pilodius*) the anterolateral angle is markedly expanded, forming a flange that can completely block the orbital hiatus (Fig. 4). The term “blocks” denotes that the flange extends across the hiatus, touching the inner supraorbital angle. In some genera the flange is absent. In others, it is only slightly expanded. It is

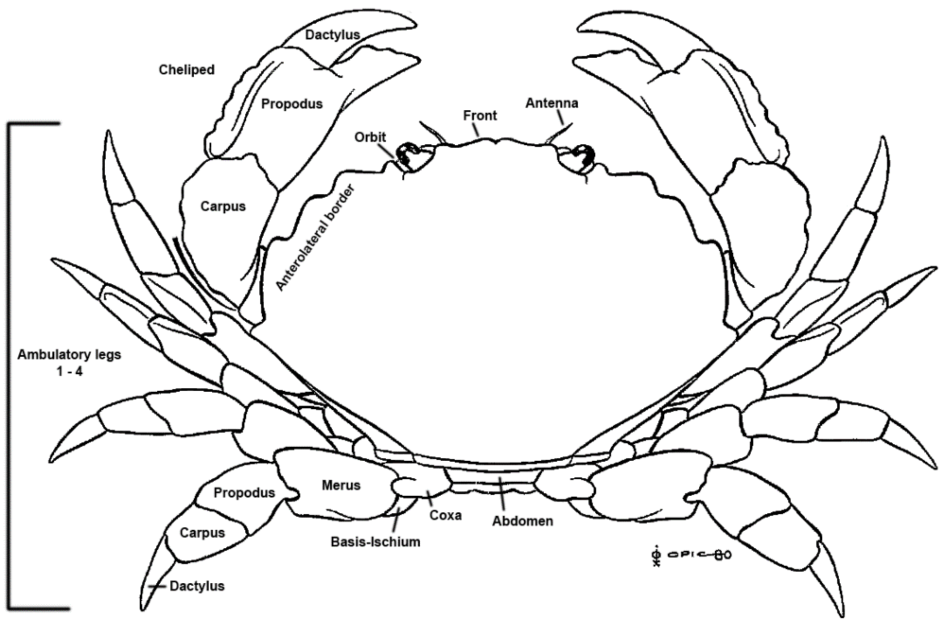

Figure 1. Dorsal anatomy of a xanthid crab, after Serène (1984: Fig. A).

important to note that this feature varies with age and size, so comparisons must be made between adult specimens only.

The other character in question is the morphology of the dactylus of the ambulatory legs. In many chlorodiellines, dactylus is clearly bifid, with one distal, pigmented tip and one subdistal, non-pigmented, downward-pointing (perpendicular) tip. The size of the subdistal tip has been historically useful for generic placement, although its utility is questionable in some cases (Ng & Yang 1998, fig. 7) (see Chapter 3). In some species, the distal, pigmented tip is reduced, and in yet others, the subdistal, non-pigmented tip is reduced, or two are present. In these cases, the use of the word “distal” or “terminal” may be confusing. However, here the pigmented tip is always referred to as the “terminal” or “distal” tip. Even when it is reduced, the pigmented tip is always distally located and confluent with the angle of the dactylus (rather than abruptly curving downwards).

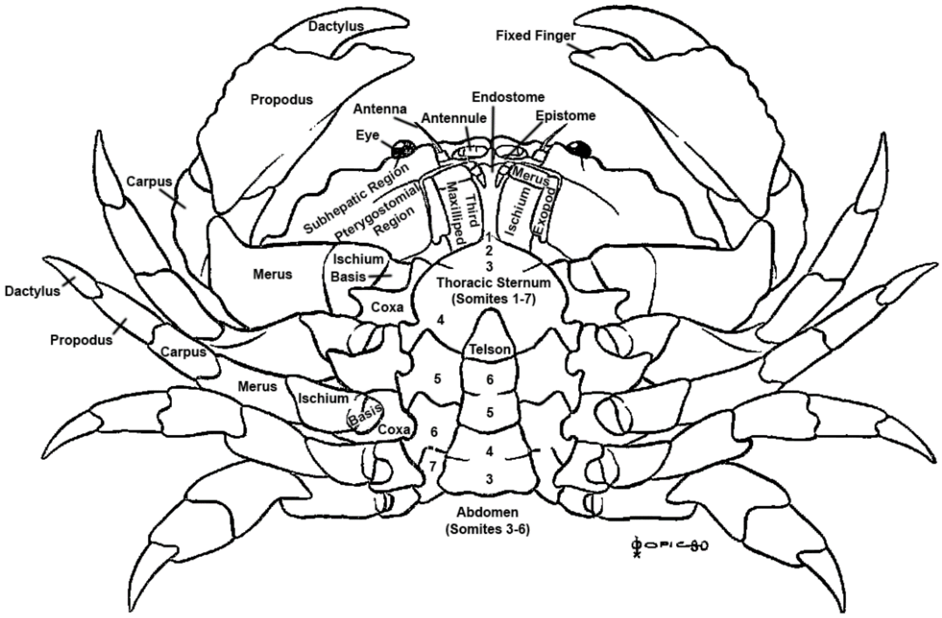

Figure 2. Ventral anatomy of a xanthid crab, after Serène (1984: Fig. B).

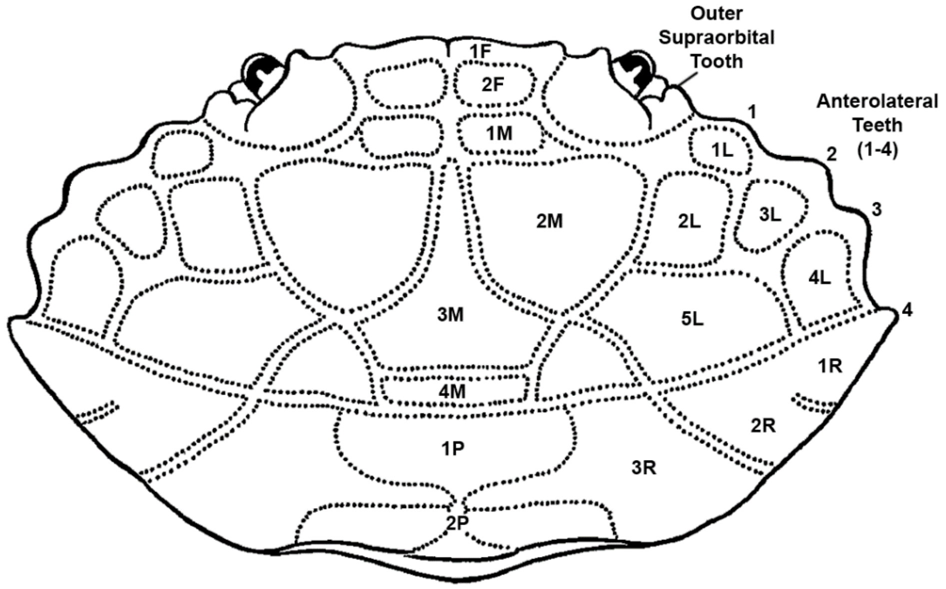

Figure 3. Carapace regions of a xanthid crab, numbered after Serène (1984: Fig. C). F, M, L, R, and P indicate frontal, median, anterolateral, posterolateral, and posterior regions, respectively.

Phylogenetics

Seven phylogenetic trees are presented in this work (Figs 5, 14 & 15) The first tree was generated using four molecular markers (12S rRNA gene, 16S rRNA gene, COXI, and H3) to delimit Chlorodiellinae from other xanthid subfamilies, and chlorodielline genera from each other (Fig. 5). Sequences generated for this study were combined with previously published xanthid sequences from Lai *et al*. (2011). This tree was used to support the removal and description of *Ratha* Lasley, Lai & Ng, 2013 (Chapter 4). Following this tree, COXI trees for each of the five chlorodielline genera were generated to aid in species delimitation (Chapter 5) (Fig. 14). Subsequently, representatives from each major clade in the COXI analyses were selected. The remaining molecular markers (12S rRNA gene, 16S rRNA gene, and H3) were then sequenced for each of these representative clades and analyzed. The resulting phylogeny more thoroughly represents chlorodielline evolutionary relationships, and generic and specific boundaries (Chapter 5) (Fig. 15). Specific methods and procedures used for chapters 3, 4, and 5 are detailed in respective chapters.

Scanning Electron Microscopy

Mucus and debris were removed from G1s, following Felgenhauer (1987). Samples were dehydrated through a graded ethanol series, followed by two changes in HMDS (hexamethyldisilazane). The specimens were subsequently mounted on stubs using Elmer's glue and then coated with 25 nm 60:40 gold: palladium using a Cressington Sputter Coater 108auto. Images were produced using a Leica Stereoscan 440.

CHAPTER 3.

PHYLOGENETIC RELATIONSHIPS OF THE CHLORODIELLINAE WITH DESCRIPTION OF TWO NEW GENERA

Introduction

The taxonomy of most of the 16 xanthid subfamilies is in serious need of revision based on morphology and molecular phylogenetics, including the Chlorodiellinae (Ng et al. 2008, Lai et al. 2011, Mendoza & Guinot 2011, Mendoza & Manuel-Santos 2012, Mendoza et al. 2012, Lasley *et al* 2015). The subfamilies have been in flux since Balss' (1957) foundational treatment of Xanthidae, with a few taxonomists making the bulk of the incremental advancements to the taxonomy. Serène (1965, 1968) aided in organization of the subfamilies by listing several genera in their respective subfamilies [Actaeinae, Chlorodiinae (= Chlorodiellinae), Cymoida (= Cymoinae), Euxanthoida (= Euxanthinae), Polydectinae, Xanthinae, Zalasiinae, and Zosimoida (Zosiminae)]. Notably, Guinot (1968, 1971, 1976, 1977a, 1978) redefined and delineated these subfamilies in a series of important publications on classification of the brachyura. She noted that the traditional morphological characters used at the time, such as carapace shape and dentition, cheliped, and ambulatory leg characters, were less informative than characters of the sternum and genital openings (Guinot 1970, Lai *et al*. 2011). Sakai and Takeda also contributed to the subfamilial classification in several concurrent works (Sakai 1976, Takeda 1973, 1976, Takeda & Miyake 1969).

In addition to the treatment of the aforementioned subfamilies, Sakai (1976) described Liomeroida (= Liomerinae). Later, Serène (1984) solidified the subfamilial taxonomy by providing a key, diagnoses, and literature reviews for 10 subfamilies in his “classic” monograph of xanthoids from the Red Sea and Indian Ocean.

More recently, several subfamilies have been described for a few aberrant genera. Kraussiinae Ng, 1993 was described for *Kraussia* Dana, 1852 and *Palapedia* Ng, 1993; Antrocarcininae Ng & Chia, 1994 was described to accommodate *Glyptocarnicus* Takeda, 1973 and the two new genera *Antrocarcinus* Ng & Chia, 1994 and *Cyrtocarcinus* Ng & Chia, 1994; and the monogeneric Speocarcininae Stevcic, 2005 was described for *Speocarcinus* Stimpson, 1859. Two further monogeneric subfamilies were subsequently described stemming from a phylologenetics study of the family (Lai *et al*. 2011): Glyptoxanthinae Mendoza & Guinot, 2011 and Garthiellinae Mendoza & Manuel-Santos, 2012.

Several publications have noted that the boundaries between many xanthid subfamilies is nebulous. Ng *et al*. (2008) noted that Euxanthinae, Actaeinae, Liomerinae, Xanthinae, and Zosiminae are poorly defined. They also treated Cymoinae, Chlorodiellinae and Etisinae separately and stated that the delineation of the latter two subfamilies is not always clear. Subsequent phylogenetics studies have come to the same conclusion. Lai *et al*. (2011) provided the first phylogeny of the family including 139 xanthid species and extensive morphological comparisons of adults and larvae. Among many polyphyletic subfamilies, Chlorodiellinae was recovered in two separate clades, although only four chlorodielline genera were included. Etisinae was recovered in three clades. Later, Lasley *et al*. (2013) provided a preliminary phylogeny of Chlorodiellinae which included members of 13 xanthid subfamilies and six chlorodielline genera. Chlorodiellinae was again recovered polyphyletic, with the six genera in five clades. However, support values for backbone clades were low and only 18 chlorodielline and 1 etisine species were included in the analyses. Thus, the subfamilial and generic limits of the subfamily remained tenuous.

Here, chlorodielline taxa are analyzed within a framework of Lai *et al.*'s (2013) previously published xanthid sequences to emphasize the subfamily's polyphyletic state. The subfamily is restricted to a well-supported monophyletic clade and redefined based on a suite of morphological characters, and two new genera are described. Chlorodielline genera outside of this clade are regarded as *incertae sedis* for the time being. For convenience, diagnoses of all chlorodielline genera, including new taxa, are presented in this chapter. Species-level taxonomy of these genera is presented later, in Chapter 5, as part of a full taxonomic revision. Furthermore, the phylogenetics section of the present chapter indicates that *Chlorodiella longimana*, the only Western Atlantic Ocean chlorodielline species, not only should be removed from the genus, but from the Chlorodiellinae as well. Chapter 4 deals with the taxonomy of this species including a description of a new genus and redescription of the species.

Material and Methods

<u>Taxon sampling</u>

Two hundred two specimens representing 189 nominal species, 89 genera, and 14 xanthid subfamilies were selected for the molecular analyses. All eight chlorodielline genera were represented and 37 of 48 chlorodielline species were included. Of the 11 missing species, five are likely junior synonyms of included species. These include: *Chlorodiella crispipleopa* Dai, Yang, Song & Chen, 1986 [= *Chl. cytherea* (Dana, 1852)]; *Pilodius cephalalgicus* Clark & Galil, 1993 [= *P. pilumnoides* (White, 1848)], *Pilodius concors* Clark & Galil, 1993 [*P. pilumnoides* (White, 1848)], *Pilodius philippinensis* (Ward, 1941) (= *P. granulatus* Stimpson, 1858); and *Tweedieia brevidactyla* Dai & Yang, 1998 [= *T. odhneri* (Gordon, 1934)] (see Chapter X). Furthermore, three taxa ([*Chlorodiella quadrilobata* Dai, Cai & Yang, 1996; *Cyclodius perlatus* (Nobili, 1905); and *Pilodius kauaiensis* Edmondson, 1962]) are poorly known species that have been recorded only in original descriptions. *Etisus maculatus* (Stimpson, 1860) was erroneously placed in two genera: *Etisus* H. Milne Edwards, 1834, and *Cyclodius* (Ng *et al*. 2008: 197, 198); but it probably belongs in *Etisus*, at least on the basis of morphology—i.e., the prominent front (Stimpson, 1860, Guinot 1969).

Most of the non-chlorodielline taxa were taken from Lai *et al*. (2011) via GenBank. The sequences generated for this study are recorded in SM 6. Seven additional etisine species were added, as the taxon is morphologically similar to Chlorodiellinae (Ng & Yang 1998, Clark & Ng 1999, Ng *et al*. 2008) and tends to group with the Chlorodiellinae in previous molecular phylogenetic studies, albeit with low support (Lai *et al*. 2011, Lasley *et al*. 2013). *Menippe rumphii* (Menippidae), *Benthochascon hemingi* (Portunidae), *Trapezia cymodoce*, and *Quadrella coronata* (Trapeziidae) were selected as outgroups following Lai *et al*. (2011). The following abbreviated subfamilial and familial names are used for clades recovered in phylogenetic analyses presented here that are congruent with clades recovered in Lai *et al.* (2011): Eux (= Euxanthinae), Lio (= Liomerinae), Xan (= Xanthinae), Act (= Actaeinae), Zos (= Zosiminae), Pol (= Polydectinae), Cym (= Cymoinae), Pse (= Pseudorhombilidae), Pan (= Panopeidae), and Chl (= Chlorodiellinae).

Analyses

Both single gene trees—to examine congruence between loci—and trees based on the concatenated data set were generated. A total of 753 mitochondrial (12S rRNA gene = 199, 16S rRNA gene = 200, COXI =170) and nuclear (H3 = 184) sequences were used for the analyses, of which 151 were generated for this study (SM 6); the remaining sequences were previously published and obtained from GenBank (Lasley *et al*. 2013, Lai *et al*. 2011). These markers were chosen so that the new species could be run with the previously published xanthid phylogeny of Lai *et al*. (2011). New sequences were amplified following Thoma *et al*. (2009) (12S and 16S rRNA genes), Buhay *et al*. (2007) (12S rRNA gene), Lai *et al*. (2009) (16S rRNA gene) Colgan *et al*. (1998) (H3), Thoma *et al*. (2013) (COXI), and Geller *et al*. (2013) (COXI). Since these publications apply several differing primer and PCR profile combinations, optimized combinations using Promega PCR Master Mix are provided. The most successful primers used were: 12sf and 12slr (12S) (Buhay *et al*. 2007); crust16sf1 and crust16sr2 (16S) (Lai *et al*. 2009); jgHCO2198 and jgLCO1490 (COXI) (Geller *et al*. 2013); and H3af and H3ar (H3) (Colgan *et al*. 1998). Reactions were carried out using the following PCR cycling parameters: initial denaturation at 95 °C for 5 min; 4 cycles at 94°C for 30 s, 57°C (12S), 52°C (16S), 50°C (COXI), 50°C (H3) for 45 s, 72°C for 1 min; then 34 cycles at 94°C for 30 s, 52°C (12S), 47°C (16S), 45°C (COXI), 47°C (H3) for 45 s; and a final extension at 72°C for 8 min. All new sequences were submitted to GenBank (Table 1). COXI and H3 sequences were checked for stop codons.

Alignments were generated with MUSCLE (Multiple Sequence Comparison by Log-Expectation) (Edgar 2004) using the default settings in Geneious version 7.1.4 (Biomatters Ltd.), and checked by eye. The length of the aligned and concatenated dataset was 1843 bp (12S rRNA = 443 bp, 16S rRNA = 490, COXI = 582, and H3 = 328) and was partitioned according to locus. Protein coding genes H3 and COXI were translated to check for stop codons.

Phylogenetic trees were inferred from the concatenated dataset using maximum-likelihood (ML), maximum parsimony (MP) and Bayesian Inference (BI) methods. Prior to the analyses, substitution models for each partition were selected using the Akaine information criterion implemented in JMODELTEST version 2.1.4 (Posada 2008). Likelihood trees were generated using Randomized Accelerated Maximum Likelihood (RAxML) version 7.7.7 (Stamatakis, 2014). COXI and H3 were partitioned by codon. The gamma model of rate heterogeneity was selected based on AIC scores, and the remaining parameters were estimated by RAxML. Confidence was assessed using 1000 non-parametric bootstrap replicates. As the deeper splits within the resulting ML-tree are not well supported (see Chapter 3) and therefore the monophyly of Chlorodiellinae (*s. lat.*) cannot be rejected, the topology found by the ML analysis was tested to see if it is significantly better than a monophyletic Chlorodiellinae (*s. lat.*) Accordingly, the Chlorodiellinae (*s. lat.*) was constrained to monophyly in RAxML and compared with the best trees of the constrained and unconstrained [Chlorodiellinae (*s. lat.*) polyphyletic] analyses with the log likelihood test (SH-test) as implemented in RAxML.

The BI analyses were carried out using MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003) on the computer cluster of CyberInfrastructure for phylogenetic RESearch project (CIPRES) (Miller *et al*. 2011). Eight chains total were run with three hot chains and one cold chain per run. The temperature was set to 0.2. Trees were sampled every 1000 generations for 50 million generations. The first 2000 trees were discarded as burn-in. Clade support was assessed with posterior probabilities (pP). Convergence of the two runs was confirmed using Tracer version 1.5 (Rambaut & Drummond 2009). The average standard deviation of split frequencies in the Bayesian analyses reached 0.009121 after 50 million generations.

The MP analyses were performed using POY 5.0.0 Beta (Varon *et al*. 2010). POY was run using the Simple Search option. The pre-aligned option was selected so that all runs (BI, ML and MP) would be comparable. Node support was assessed using 1000 bootstrap replicates.

Results

Models selected by JModeltest version 2.1.4 for COXI, 12S and 16S rRNA genes, and Histone H3 were TrN+I+G, HKY+G, HKY+I+G, and K80+G, respectively. The separate gene trees did not provide support—i.e., greater than 0.95 pP or 70 BS—of phylogenetic relationships for most nodes above sister species pairs. The deeper nodes with high support were generally in agreement with the concatenated dataset. There were three notable exceptions: 1) a clade recovered in the COXI-only BI analysis comprising *Pilodius areolatus* (H. Milne Edwards, 1834), *P. moranti* Clark & Galil, 1933, *Soliella flava* (Rathbun, 1894), comb. nov., and *S. melanospinis* (Rathbun, 1911), comb. nov. (pP = 0.96) (versus *P. areolatus* and *P. moranti* with the other *Pilodius* species in the combined dataset) (SM 1); 2) a clade recovered in the COXI-only BI analysis comprising *Pilodius* and *Cyclodius*, but excluding *Cyclodius obscurus* (pP = 1) (versus *Cyc. obscurus* included in the combined dataset) (SM 1); and 3) a clade recovered in the H3-only ML and BI analyses comprising *Chlorodiella cytherea*, *Chl. davaoensis* and *Chl. clymene* (pP = 1, BS = 92) (versus *Chl. clymene* sister to *Chl. nigra* and *Chl. xishaensis* in the combined dataset) (SM 2, SM 3). These clades were not supported in any other single gene analysis. All analyses (BI, ML, and MP) produced similar trees with differences in nodes with low support (Fig. 5). Most of the non-chlorodielline taxa from Lai *et* al. (2011) were recovered in clades congruent with their findings (i.e., Act 1, 2, 3; Chl 2; Cym; Eux 1, 3; Lio 1, 2; Pol; Xan 1, 3, 4, 10; Pan+Pse+Spe+Xan 6+Xan7+Xan 8; and Zos 1, 2). The log likelihood test showed that the constrained topology [Chlorodiellinae (*s. lat.*) monophyletic] is not significantly worse than the best topology found by the ML analysis ($p<0.01$).

The three most species rich chlorodielline genera (*Chlorodiella*, *Pilodius*, and *Cyclodius*) were recovered in a well-supported, monophyletic clade (pP = 1.00, ML BS = 87, but MP BS < 50). Although, two novel lineages were recovered comprising members of *Pilodius*. Furthermore, one member of *Pilodius*, *P. paumotensis*, was recovered in a well-supported clade with members of *Cyclodius* (see below). The remaining chlorodielline genera, *Ratha*, *Liocarpilodes*, *Tweedieia*, *Sulcodius*, and *Vellodius*, were recovered outside of this clade, in various positions with other subfamilies. *Sulcodius* was sister to *Etisus laevimanus* Randall, 1840 (Fig. 5: *Etisus* 1), but only in the BI analysis and with low support (pP = 0.93). *Ratha longimana* (H. Milne

Figure 5. Bayesian consensus tree Xanthidae inferred from combined 12S, 16S, COXI, and H3 sequences. Catalog numbers are included. Numbers above, below left, and below right indicate Bayesian Inference posterior probability (pP), maximum likelihood bootstrap support (ML BS), and maximum parsimony bootstrap (MP BS) support, respectively. The latter two support values are separated by "/". Values below 95 (pP) and 70 (ML BS and MP BS) are represented by "–". Missing bootstrap values indicate clades not recovered in ML or MP analyses. Red indicates chlorodielline (s.l.) taxa. Brown indicates *Etisus* taxa. Other colored taxa are Chlorodiellinae (s.s.). Three-letter abbreviations correspond with clades of the same name and sequences in Lai *et al*. (2011).

Edwards, 1834) grouped with "Xan 5" species though not supported (pP = 0.78, ML BS < 50) in the BI and ML analyses. Similarly, *Vellodius etisoides* (Takeda & Miyake, 1968) was recovered sister to *Etisus sakaii* Takeda & Miyake, 1968, *E. frontalis* (Dana, 1852), and *E. electra* (Herbst, 1801) with low support (pP = 0.79, not recovered in the ML and MP analyses). However, its sister clade (Fig. 5: *Etisus* 2) is well supported (pP = 1, ML BS = 89, MP BS = 72).

The analyses indicate that *Liocarpilodes* is polyphyletic. *Liocarpilodes integerrimus* (Dana, 1852) fell in a clade with moderate support (pP = 0.97, ML BS = 54, not recovered in MP), sister to several etisines [*Etisus bifrontalis* (Edmondson, 1935), *E. odhneri* Takeda, 1971, *E. demani* Odhner, 1925, and *E. albus* (Ward, 1934) = *Etisus* 4]. *Liocarpilodes harmsi* (Balss, 1934) grouped with “Zal” [*Zalasius dromiaeformis* (De Haan, 1839) and *Z. sakaii* Balss, 1938] in a clade with low support (pP < 0.50) that was only recovered in the BI analysis. *Liocarpilodes armiger* (Nobili, 1905) and *L. pacificus* Balss, 1938, were recovered as sister species (pP = 1, ML BS = 100, MP BS = 100) in a deeper clade with low support (pP < 0.50) that was not recovered in the ML or MP analyses.

Beyond the aforementioned relationships of *Etisus*, another clade was recovered comprising *E. villosus* Clark & Galil, 1995, *E. splendidus* Rathbun, 1906, *E. utilis* Jacquinot, 1853, *E. dentatus* (Herbst, 1785), and *E. anaglyptus* H. Milne Edwards, 1834 (Fig. 5: *Etisus* 3) with relatively high support values (pP = 0.99, ML BS = 88, but MP BS < 50). In total, the included *Etisus* species separated into four distinct clades, generally with high support values.

Within the large chlorodielline clade [Chlorodiellinae (*s. str.*)], *Chlorodiella* was recovered in a monophyletic clade with high support (pP = 1, ML BS = 98, MP BS = 87). *Pilodius* and *Cyclodius* were polyphyletic. Four species of *Pilodius* [*P. spinipes* Heller, 1861, *P. pugil* Dana, 1852, *P. scabriculus* Dana, 1852, and *P. pubescens* Dana, 1852 (= *Luniella*, gen. nov.)] formed a well-supported (pP = 1, ML BS = 99, MP BS = 86) clade, sister to *Chlorodiella*. The remaining species in this clade were recovered in a well-supported clade (pP = 1, ML BS = 97, MP BS = 99). Within this clade, three subclades were recovered: 1) *P. melanospinis* and *P. flavus* (*Soliella*, gen. nov.) (pP = 1, ML BS = 100, MP BS = 100); 2) *P. miersi* (Ward, 1936), *P. granulatus* Stimpson, 1858, *P. nigrocrinitus* Stimpson, 1858, *P. maotieni* Serène, 1971, *P. concors* Clark & Galil, 1993, *P. pilumnoides* (White, 1848), *P. moranti*, and *P. areolatus* (*Pilodius*) (pP = 0.94, ML BS = 52, not recovered in MP); and 3) *Cyc. ungulatus* (H. Milne Edwards, 1834), *Cyc. obscurus* (Hombron & Jacquinot, 1846), *P. paumotensis* Rathbun, 1907, *Cyc. nitidus* (Dana, 1852), *Cyc. granulosus* De Man, 1888, *Cyc. granulatus* (Targioni-Tozzetti, 1877), and *Cyc. drachi* Guinot, 1964 (*Cyclodius*) (pP = 1, ML BS = 94, MP BS = 57).

In summary, the Chlorodiellinae (*s. str.*) now comprises five genera: *Pilodius, Cyclodius*, *Chlorodiella*, *Luniella*, and *Soliella*. The remaining genera are regarded as *incertae sedis* for the time being (see Remarks for Chlorodiellinae, and General Discussion and Conclusion).

Discussion

The decision to restrict Chlorodiellinae to *Chlorodiella*, *Cyclodius*, *Pilodius*, *Luniella* gen. nov., and *Soliella* gen. nov., while provisionally transferring the other genera to *incertae sedis* was made with some hesitation. Given the high support for the new chlorodielline clade and cohesive morphology of this group to the exclusion of the removed genera, it was clear that these genera had to be withdrawn (Fig. 5). The problem, then, was the unresolved state of the many xanthid subfamilial boundaries, obvious in the molecular analysis with Etisinae, and several other subfamilies, divided and scattered throughout the xanthid phylogeny. There were two options: treat *Tweedieia*, *Ratha*, *Sulcodius*, *Vellodius*, and *Liocarpilodes* as *incertae sedis*, or place them tentatively in other subfamilies. The former was chosen as a compromise solution and in concordance with the constrained topology test.

The topology of the present xanthid tree indicates a monophyletic Chlorodiellinae, including *Pilodius*, *Cyclodius*, *Chlorodiella*, *Soliella*, gen. nov., and *Luniella*, gen. nov., but excluding *Liocarpilodes*, *Ratha*, *Sulcodius*, *Tweedieia*, and *Vellodius* (Fig. 5). Two characters, spoon-like tips of the fingers of the claws and a dactylo-propodal locking mechanism on the walking legs, have historically been used to unite members of Chlorodiellinae and Etisinae. However, the utility of these supposedly diagnostic features was called into question recently (Lai *et al.*, 2011; Ng *et al*., 2008). The present phylogenetic analyses indicate that these characters are indeed paraphyletic and have evolved independently in different lineages. The Chlorodiellinae is redefined here and delimited based on a new suite of characters.

The genus *Liocarpilodes* is clearly polyphyletic, with members segregating into three clades that possess strikingly different morphological features used in xanthid taxonomy to define genera—e.g., characteristics of the male abdomen, thoracic sternum, and G1; spination of the chelipeds; morphology of the tip of the ambulatory dactylus; and morphology of the anterolateral margin of the carapace. Based on the phylogeny, *L. integerrimus* is allied with *Etisus bifrontalis*, *E. odhneri*, *E. demani*, and *E. albus* (*Etisus* 4) with moderate support (pP = .97, ML BS = 54, not recovered in MP). *Liocarpilodes armiger* and *L. pacificus* are well-supported (pP = 1, ML BS = 100, MP BS = 100) sister species, but their relationship with other xanthid genera is not resolved. The same is true for *L. harmsi.* The only *Liocarpilodes* species not included was *L. biunguis*. Given the almost indistinguishable G1s, and similar sterna and abdomen, *L. biunguis* is likely allied with *L. harmsi*. Further commentary is beyond the scope of this study, except to say that *Liocarpilodes* likely comprises three genera and is in need of taxonomic revision.

Etisinae, as currently defined (Ng *et al*., 2008), comprises only two genera: *Etisus* and the monotypic *Paretisus* Ward, 1933. However, the topology of the xanthid phylogeny indicates that *Etisus* represents at least three independent lineages (Results; see also Lai *et al.*, 2011: 434), each defined by suites of uniting morphological characters. The members of *Etisus* 2 that were sampled for the analyses have a well-developed dactylo-propodal locking mechanism and a strikingly long male thoracic sternum (Fig. 7E). *Etisus* 3 specimens are united by their reduced dactylo-propodal locking mechanism and comparatively shorter, broader male thoracic sternum (Fig. 7F). These features vary or are unknown in *Etisus* 4, but members of the clade are united by a conserved G1 morphology—i.e., long and narrow, without stout, long distal setae. In summary, the Etisinae, as presently defined, is also in need of revisionary work and likely comprises several genera.

These taxa have historically been associated with the Chlorodiellinae, but their placement now is uncertain. The type species of *Liocarpilodes*, *L. integerrimus*, was recovered with *Etisus* 4 (pP = 0.97, ML BS < 70), so the genus may end up in Etisinae pending necessary revisions of *Liocarpilodes* and Etisinae. *Vellodius* and *Sulcodius* grouped with *Etisus* 2 and *Etisus* 1, respectively, in the combined BI analysis, albeit with low support. Based on these data and the taxa's similar transversely hexagonal carapaces, spoon-like tips of the chelae, and dactylo-propodal locking mechanisms on the ambulatory legs, these genera are probably close to *Etisus s. lat.* Greater taxon sampling of Etisinae for morphological comparisons (e.g., investigating male sternal and male gonopod characters) and molecular phylogenetics will undoubtedly be necessary and insightful. The same is true of *Tweedieia*.

Systematic Account

Subfamily Chlorodiellinae Ng & Holthuis, 2007

(see synonymy, Ch. 5)

Genera included. *Chlorodiella* Rathbun, 1897; *Cyclodius* Dana, 1851; *Pilodius* Dana, 1851; *Luniella* gen. nov.; *Soliella* gen. nov.

Diagnosis. Carapace transversely hexagonal (Fig. 6). Anterolateral margin relatively straight. Front arched or sinuous; not produced. Chelipeds subequal. Fingers gaping, tips spoon-like. Merus with anterior margin smooth, granulate, or with short spines or teeth; dorsal surface without deep longitudinal sulcus. Male thoracic sternum broad (Fig. 7). Anterior margin of telson reaching beyond imaginary line between posterior margin of first ambulatory leg sternal condyles, not reaching more than halfway between sutures of sternites 2-3 and 4-5. Episternites 6, 7 not delimited by sulcus. Abdominal somite 3 not locking with thoracic episternite 7. Ambulatory legs moderately long; dactylo-propodal locking mechanism well developed; pigmented, distal spine of dactylus roughly equal to or longer than subdistal spines. G1 tip spatulate, tubular, hooked, curled, recurved or flat; often with stout, proximally-directed subdistal setae, sometimes with long subdistal setae (Figs 8, 9).

Remarks. The present definition of Chlorodiellinae excludes *Ratha*, *Vellodius*, *Sulcodius*, *Liocarpilodes*, and *Tweedieia*. As defined here, chlorodiellines have a distinct transversely hexagonal carapace without conjoined, transverse granules on anterior regions; a broad thoracic sternum; a telson reaching beyond the imaginary line between the posterior margin of the first ambulatory leg condyles; relatively short chelipeds without a

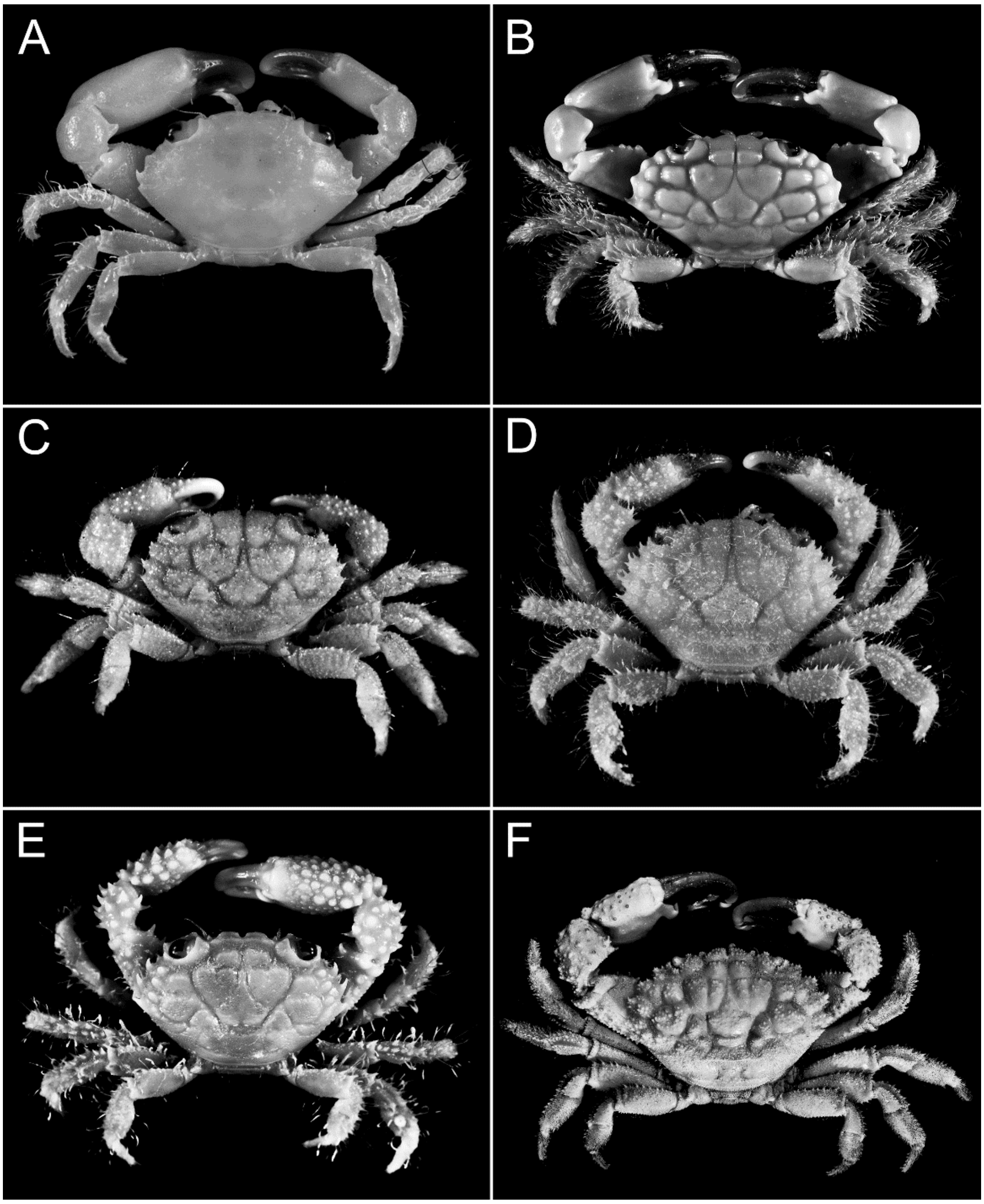

Figure 6. Dorsal habitus of representative chlorodielline (*s. str*.) genera: A – *Chlorodiella laevissima* (Dana, 1852) (UF 13733); B – *Cyclodius nitidus* (Dana, 1852), 23.8 × 14.3 (USNM 154905); C – *Cyclodius paumotensis* (Rathbun, 1907), holotype, 8.0 × 5.3 (USNM 32852); D – *Soliella flavus* (Rathbun, 1894), 10.2 × 6.9 (USNM 1181377); E – *Luniella pugil* (Dana, 1852), 11.4 × 7.4 (USNM 33412); F – *Pilodius concors* Clark & Galil, 1993, holotype, 62.25 × 42.00 (ZRC 1965.11.11.147).

longitudinal sulcus or row of large teeth of roughly equal size on the merus; and dactyli of the ambulatory legs with a pigmented tip that is equal to or longer than accessory, non-pigmented tip(s) (Figs 6–9). *Vellodius, Sulcodius* and *Ratha* resemble chlorodielline genera in having a similarly shaped transversely hexagonal carapace, a non-projecting front, chelar fingers with spoon-like tips, and well-developed dactylo-propodal locking mechanisms of the ambulatory legs (Ng & Yang 1998: figs 1–3, 7; Clark & Ng 1999: figs 1, 2, 7; Lasley *et al*. 2013: figs 2–4). However, *Vellodius* differs from chlorodielline genera in having a relatively narrow, long male thoracic sternum; a telson of the male abdomen with an anterior margin not reaching beyond the imaginary line between the posterior margin of first ambulatory leg sternal condyles; transverse striae of the anterior and posterior regions of the carapace; and a bifid tip of ambulatory leg dactylus with a non-pigmented tip that is longer than the pigmented tip (Takeda & Miyake 1968: 186, fig. 2, pl. 8c,d; Ng & Yang 1998: figs 1, 2A,B, 3B, 7D) [vs. broad thoracic sternum; male abdomen with telson reaching beyond line; no anterior transverse striae of the carapace; and a pigmented tip longer or equal to the non-pigmented tip in Chlorodiellinae] (Figs 6, 7). *Vellodius* also has a distinct G1 morphology (truncate and bearing two long, distal setae) not seen in Chlorodiellinae (Ng & Yang 1998: fig. 4A–D) (Figs 8, 9).

Sulcodius differs from the chlorodielline genera by its long, relatively narrow chelipeds with a deep, longitudinal grooved merus; and vestigial pigmented tip of the ambulatory leg dactylus (Clark & Ng 1999: figs 1, 3B, 7) [vs. shorter, stouter chelipeds (although large specimens of *Chl. nigra* are close in length) without a deep longitudinal groove on the merus; and bifid tip of ambulatory leg dactylus with a non-pigmented tip that is longer than the pigmented tip in Chlorodiellinae] (Fig. 6).

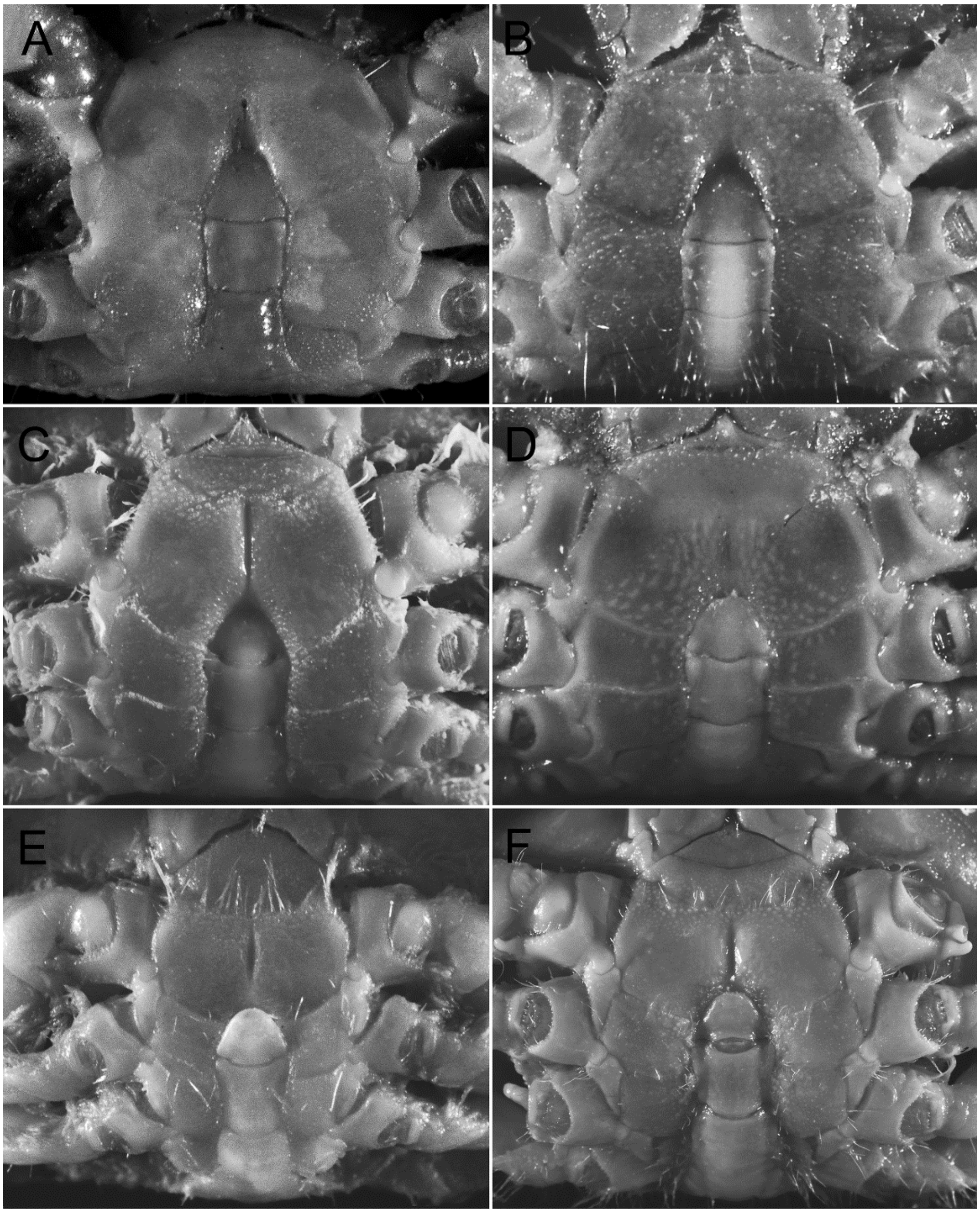

Figure 7. Male thoracic sterna of representative chlorodielline (s.l.) and related genera: A – *Chlorodiella nigra* (Forskål, 1775), 16.85 × 11.05 mm (SMF 7161); B – *Soliella flava* (Rathbun, 1894), 10.2 × 6.9 (USNM 1181377); C – *Vellodius etisoides* (Takeda & Miyake, 1968), 15.4 × 9.9 mm (ZRC 1998.50); D – *Tweedieia odhneri* (Gordon, 1934), 11.3 × 7.9 (USNM 41260); E – *Etisus sakaii* Takeda & Miyake, 1968, 10.3 × 8.2 mm (UF 16901); F – *Etisus anaglyptus* H. Milne Edwards, 1834, 34.1 × 23.0 (USNM 1014269).

Ratha is distinct from chlorodielline genera with respect to its relatively narrow orbits; long chelipeds with three large, roughly equal, acute teeth on the anterior margin; and Western Atlantic distribution (Lasley *et al*. 2013: fig. 2A–C) [vs. relatively wide orbits; short chelipeds (although similarly long in large specimens of *Chl. nigra*) with a merus that is smooth, granular, or adorned with short spines; and Indo West-Pacific distribution in Chlorodiellinae (*s. str*.) (Fig. 6)].

The similarity of chlorodiellines to *Tweedieia* and *Liocarpilodes* is primarily in possessing well-developed dactylo-propodal locking mechanisms on the ambulatory legs and spoon-tipped chelae. However, *Tweedieia* and *Liocarpilodes* differ markedly in having a transversely ovate carapace (Serène 1984: pl. 37) [vs. generally transversely hexagonal in the Chlorodiellinae (Fig. 6)]. *Tweedieia* differs further in possessing a telson of the male abdomen that almost reaches the imaginary line between the posterior margin of the first ambulatory leg sternal condyles, and very short, stout movable fingers of the chelae (Serène 1984: fig. 166; Dai & Yang 1998: fig. 1-2) [vs. telson reaching beyond the line and proportionately longer movable fingers in Chlorodiellinae (Fig. 7)]. Despite clear differences between *Liocarpilodes* species and chlorodielline genera, it is difficult to state the further distinctions generally, as *Liocarpilodes* is polyphyletic as currently defined and not morphologically cohesive (see General Discussion and Conclusion).

Subfamilial placement of *Vellodius*, *Sulcodius*, *Liocarpilodes*, *Tweedieia*, and *Ratha* is complicated, but, given the morphological and molecular data, these genera clearly do not belong in Chlorodiellinae as now defined and must be removed. Etisinae is the most obvious choice for these taxa based on superficial external morphology, although the available data strongly suggest the Etisinae is also a “mixed bag” (Fig. 5) (Ng *et al*. 2008; Lai *et al*. 2011). However, the log likelihood test indicates that the constrained topology—all chlorodiellines (*s. lat.*) monophyletic—is not significantly worse than the topology recovered in the ML tree. This result is presumably due to unresolved deep nodes. Therefore, these taxa cannot be transferred despite morphological similarity to Etisinae, high support for Chlorodiellinae excluding these taxa, and morphological evidence for their removal. Consequently, *Vellodius*, *Sulcodius*, *Liocarpilodes*, *Tweedieia*, and *Ratha* will remain *incertae sedis* pending a systematic study of Etisinae and necessary re-assessment of xanthid subfamilial boundaries.

Chlorodiella Rathbun, 1897

(see synonymy Ch. 5)

Type species. *Cancer nigra* Forskål, 1775 (by Rathbun, 1897)

Diagnosis. Carapace transversely hexagonal (Fig. 6A). Surface appearing smooth, glabrous without magnification, sometimes with minute granules or punctuations. Regions undefined medially and usually laterally, sometimes raised laterally with indistinct areolae. Front arched; anterior margin smooth, serrated or lined with minute granules; divided into two lobes by shallow notch; lobes arched or slightly sinuous. Anterolateral margin with 0, 1, 3 or 4 teeth, excluding exorbital tooth; without denticles between teeth, margins smooth or granular. Basal antennal segment without elongated

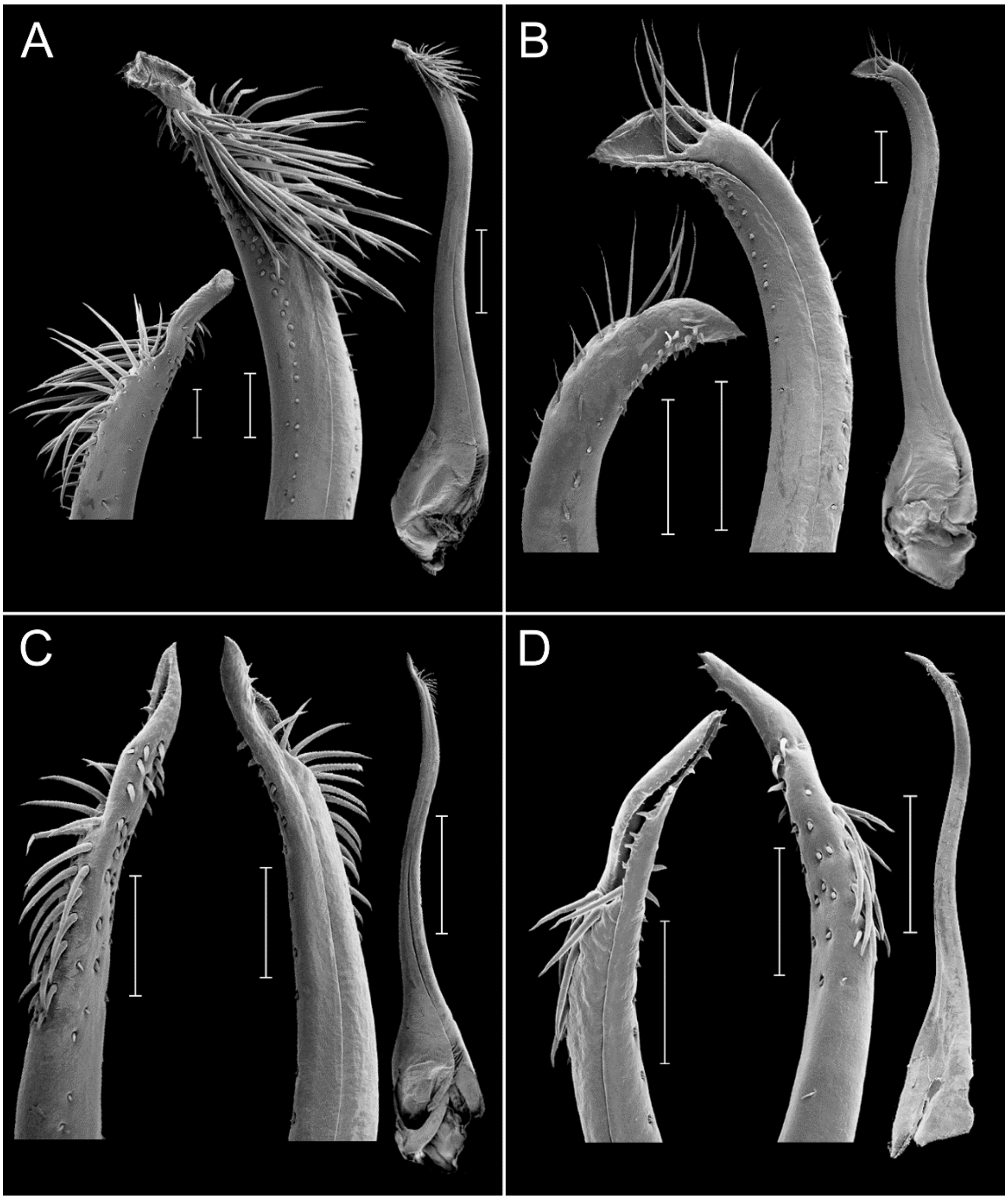

Figure 8. First male gonopods of representative chlorodielline (*s. str.*) genera. For each species, arrangement is left to right: internal (dorsal) detail, external (ventral) detail, and external full. Scale bar measurements presented left to right: A – *Cyclodius ungulatus* (H. Milne Edwards, 1834) left G1, 200um, 200um, 1mm (UF 25663); B – *Cyclodius paumotensis* (Rathbun, 1907) left G1, 200um, 200um, 200um (UF 15600); C – *Soliella flavus* (Rathbun, 1894) left G1, 200um, 200um, 1mm (UF 12254); D – *Soliella melanospinis* (Rathbun, 1911) left G1, 200um, 200um, 1mm (ZRC 2013.1647).

flange blocking orbital hiatus; flagellum free to enter orbit (Fig. 10A). Surface of chelae glabrous, smooth, free of granules or spines; tips of fingers spoon-like, deeply hollowed. Ambulatory legs long, narrow. Tip of ambulatory leg dactylus bifid; subdistal spine approximately equal in length to distal pigmented spine. G1 tip spatulate, hooked, curled, or truncate, usually with stout proximally directed setae (Fig. 9A).

Species included. *Chlorodiella barbata* (Borradaile, 1900); *Chl. cochlearis* (Zehntner, 1894); *Chl. cytherea* (Dana, 1852); *Chl. laevissima* (Dana, 1852); *Chl. martensi* (Krauss, 1843); *Chl. planapexa* sp. nov.; *Chl. nigra* (Forskål, 1775); *Chl. ohshimai* Miyake & Takeda, 1967; *Chl. quadrilobata* Dai, Cai, & Yang, 1996; *Chl. clymene* (Herbst, 1801); *Chl. xishaensis* Chen & Lan, 1978.

Remarks. The most conspicuous characteristic of *Chlorodiella* is its smooth, glabrous carapace with undefined or poorly defined regions (Fig. 6A). Large specimens of *Chl. xishaensis* and, most notably, *Chl. nigra* sometimes have raised regions of the carapace, but these are not defined by distinct areolae, as in other chlorodiellines (Serène 1984: pl. 36 B, 43 E). The raised regions of these two species are usually restricted to the lateral areas of the carapace, with a smooth or slightly defined mesial area. All other species of *Chlorodiella* have a more or less smooth carapace (Serène 1984: pl. 36).

The monotypic *Ratha* is the only genus previously classified as a chlorodielline with a similarly smooth carapace and undefined regions (Lasley *et al*. 2013: fig. 2A). Although, like *Chl. nigra* and *Chl. xishaensis*, the lateral regions are sometimes raised. However, *Ratha* differs from *Chlorodiella* in having single-tipped dactyli of the ambulatory legs, long cheliped meri with several, separated teeth, and relatively narrow orbits (Lasley *et al*. 2013: figs 2A, B, 3B, 4A) [versus bifid dactyli, no or few small teeth on the merus of the chelipeds, and wider orbits in *Chlorodiella* (Fig. 6A)]. Furthermore, *Ratha* is only known from the western Atlantic whereas all *Chlorodiella* are from the Indo-West Pacific (see Chapter 4 for detailed taxonomic account).

Pilodius Dana, 1851

(see synonymy Ch. 5)

Type species. *Chlorodius pilumnoides* White, 1848 (by Forest & Guinot 1861)

Diagnosis. Carapace transversely hexagonal (Fig. 6F). Surface granular, adorned, especially laterally, with pearliform granules or short, conical spines. Carapace with dark, long, simple setae; long, plumose setae; or short pubescence. Regions defined by deep areolae. Front sinuous, divided by relatively deep notch, comprising submedial, broad lobe and lateral narrow lobe. Anterolateral margin with four lobes, each tipped with emergent anteriorly directed spine (short conical granule in *P. areolatus*) and smaller accessory spines or granules. Basal antennal segment with elongated flange completely blocking or extending more than halfway into orbital hiatus, excluding flagellum (Fig. 10C). Superior margin of chelae granular or spinose; fingers gaping; tips spoon-like, deeply hollowed. Ambulatory legs moderately stout with numerous setae; tip of dactylus with long, distal pigmented spine; non-pigmented subdistal spines almost equal in length to minute. G1 tip spatulate, truncate, tubular, recurved or bent (Fig. 9B).

Species included. *Pilodius areolatus* (H. Milne Edwards, 1834); *P. granulatus* Stimpson, 1858; *P. maotieni* Serène, 1971; *P. miersi* (Ward, 1936); *P. moranti* Clark & Galil, 1993; *P. nigrocrinitus* Stimpson, 1858; *P. pilumnoides* (White, 1848).

Remarks. In their revision of the genus, Clark & Galil (1993) provided a thorough account of the taxonomic history of *Pilodius* and indicated that *P. pilumnoides* is the type species. Ng *et al*. (2008), however, stated, “Serène (1984: 233) was apparently the first to nominate […] that *Pilodius pubescens*

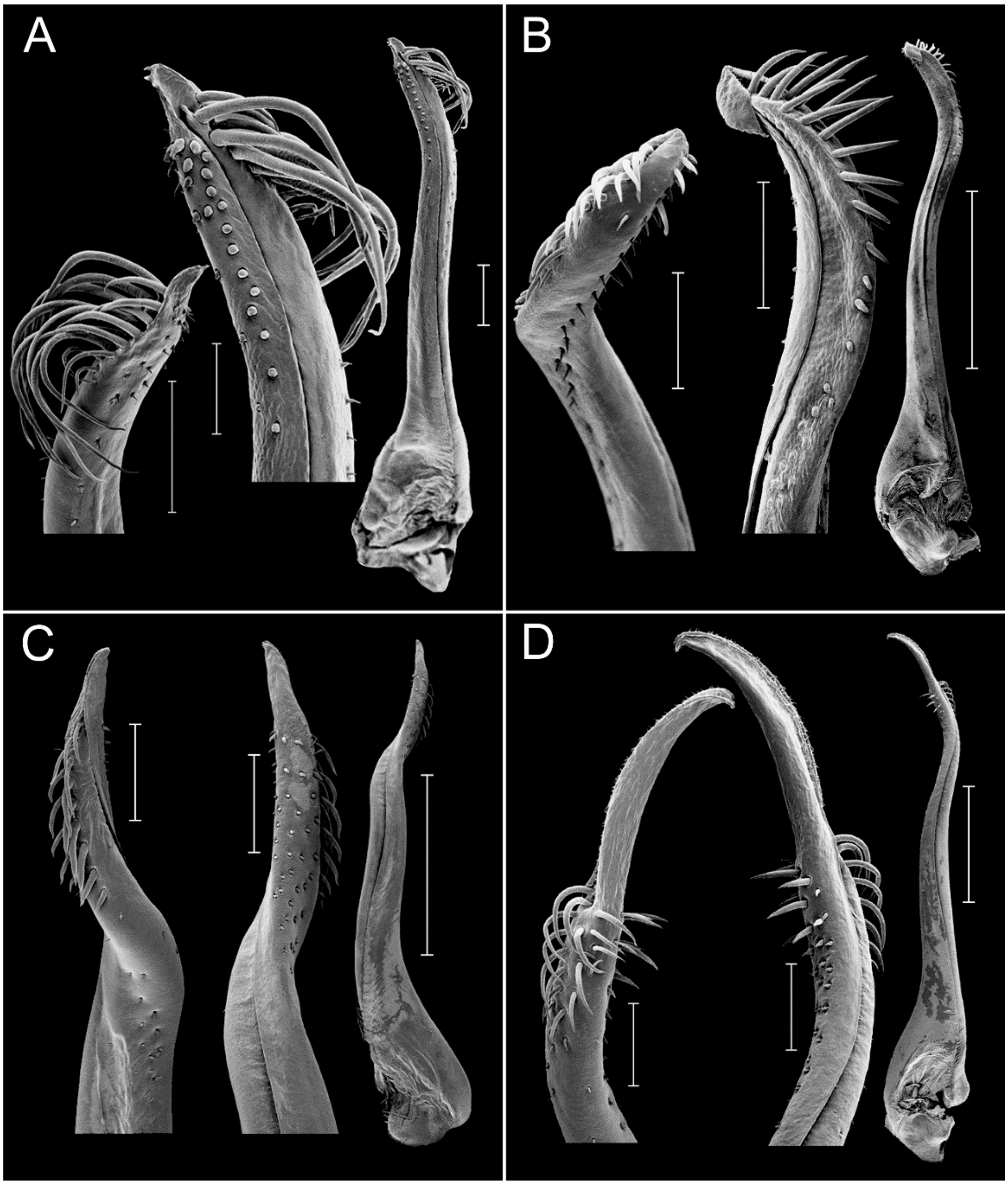

Figure 9. First male gonopods of representative chlorodielline (*s. str.*) genera. For each species, arrangement is left to right: internal detail, external detail, and external full (D is internal detail, lateral left detail, and external full). Scale bar measurements presented left to right: A – *Chlorodiella laevissima* (Dana, 1852) left G1, 200um, 100um, 200um (UF 13803); B – *Pilodius nigrocrinitus* (Stimpson, 1858) right G1 (reflected), 200um, 200um, 1mm (UF 17075); C – *Luniella scabriculus* (Dana, 1852), right G1 (reflected), 200um, 200um, 1mm (UF 1614); D – *Luniella spinipes* Heller, 1861, left G1, 200um, 200um, 1mm (UF 14361).

is the type species, and his action therefore has precedence." They further stated that the composition of the genus would not change depending on which species is the type. However, Forest & Guinot (1961: 90) had even earlier selected *Chlorodius pilumnoides* White, 1848, as type species for *Pilodius*, which has precedence. Thus, *P. pilumnoides* remains the type species of *Pilodius*.

Clark & Galil (1993: 1124) remarked that the sole character distinguishing *Pilodius* from other chlorodielline genera is the presence of a lateral flange of the basal antennal segment which blocks the orbital hiatus. They also pointed out that Crosnier had stated, as a footnote in Serène (1984: 233), that this character varies with age and that some species possess only a feeble prolongation of this flange. *Pilodius paumotensis* was the only species mentioned that does not have a fully prolonged basal antennal flange (Fig. 10D).

Given the currently included species in *Pilodius*, the utility of the basal antennal segment for generic delimitation is problematic. *Pilodius flavus* (= *Soliella flavus* comb. nov.) and *P. melanospinis* (= *S. melanospinis* comb. nov.) have basal antennal segments with a flange that generally extends less than halfway the length of the orbital hiatus (Fig. 10F). Furthermore, the flanges of *P. areolatus* and *P. miersi* do not fully block the orbital hiatus. Interestingly, molecular evidence suggests that *P. flavus* and *P. melanospinis* form a monophyletic clade sister to the remaining *Pilodius* species, with the exception of *P. paumotensis* which falls in *Cyclodius* (Fig. 5). Based on these and further morphological data, the elevation of *P. flavus* and *P. melanospinis* to a new genus, *Soliella* gen. nov., and the placement of *P. paumotensis* in *Cyclodius*, is warranted. With the rearrangements based on phylogeny and other morphological features (see below), the character works. *Pilodius*, as defined here, possesses a basal antennal flange that extends more than halfway into the orbital hiatus (usually completely blocking it), whereas *Chlorodiella*, *Soliella*, and *Cyclodius* either lack this flange, or possess one that extends less than halfway into the orbital hiatus (Fig. 10). *Luniella* gen. nov., shares this feature in common with *Pilodius* and is differentiated by other features (see Remarks for *Luniella*).

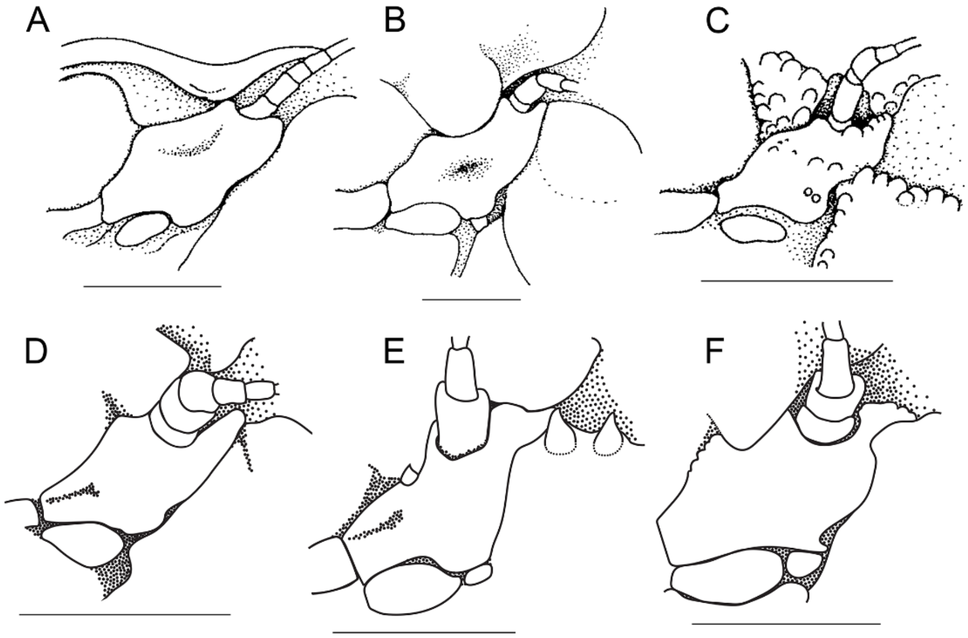

Figure 10. Basal antennal segments of representative chlorodielline (*s. str.*) genera. Scalebar = 1 mm. A–C after Ng & Yang (1998: fig. A–C): A – *Chlorodiella nigra* (Forskål, 1775) (ZRC 1998.48); B – *Cyclodius ungulatus* (H. Milne Edwards, 1834) (ZRC 1965.11.11.16); C – *Pilodius granulatus* (Stimpson, 1859) (ZRC 1998.49); D – *Cyclodius paumotensis* (Rathbun, 1907) (ZRC 1999.1211); E – *Luniella spinipes* (Heller, 1861) (UF 14361); F – *Soliella flavus* (Rathbun, 1894) (UF 12254).

The setation of the carapace, even in preserved specimens, is another important character, despite the fact that the setae can sometimes be worn, damaged or lost with age. Based on the topology of *Pilodius*, setation within the genus is phylogenetically informative. Three species in the genus (*P. maotieni*, *P. nigrocrinitus*, and *P. pilumnoides*) are covered with stout black setae on the dorsal surface of the carapace (Pls 32–34). *Pilodius areolatus*, on the other hand, has very diagnostic dense, plumose setae surrounding prominent pearliform granules (Pl. 28A, B). *Pilodius moranti* is unique—covered with short, dark setae and long, plumose light-colored setae. *Pilodius granulatus* and *P. miersi* usually bear short plumose, white or yellow pubescence; although specimens are commonly encountered with some or all of the setae removed (Pls 29, 31). None of the species, however, have a carapace densely covered with long and short yellow, simple setae like that of

Luniella pubescens, *L. spinipes* (more scattered), *Luniella*, and *Cyclodius paumotensis* (Pls 21, 24, 27, 35, 36).

Thus, *Pilodius* is differentiated from other chlorodielline genera based on the following characters: carapace adorned with dark, long, simple setae; long, plumose setae; or short pubescence (vs. glabrous or covered in short and long yellow setae in other chlorodiellines); flange of basal antennal segment completely filling or extending more than halfway into orbital hiatus (vs. flange absent or extending less than halfway in all genera except *Luniella* gen. nov.) (Fig. 10); and G1 with spatulate, truncate, tubular, recurved or bent tip (vs. tip conserved tubular or spatulate in *Soliella* gen. nov., or conserved sickle-shaped in *Luniella* gen. nov.) (Figs 8C, D, 9B–D).

The identity of *P. kauaiensis* Edmondson (1962) is contentious. Edmondson (1962) stated that this species looks like a juvenile *Neoliomera*, but placed *P. kauaiensis* in *Chlorodopsis* (= *Pilodius*) "tentatively" because "the breadth of the frontal margin seems to exclude them from that genus." He based his description on two ovigerous females, 8 mm and 9 mm broad. Based on his description and figure, the species is unlikely a *Pilodius*. Clark & Galil (1993: 1159) examined the type material of this specimen at the Bernice P. Bishop Museum and concluded, based on its lack of a basal antennal flange, that *P. kauaiensis* had been assigned to *Pilodius* erroneously. Later, Ng *et al.* (2008: 207) stated that the "antennal structure and general carapace features indicate that (the holotype) is not a pilodiine, and may warrant its own genus, but male abdominal and gonopod characters will need to be examined before its taxonomic status can be clarified." The regions are not indicated, the carapace is not adorned with setae, and the anterolateral teeth are not indicated, as in *Pilodius*. The species is quite similar to *Liocarpilodes biunguis* (Rathbun, 1906) and may be a junior synonym. In any event, *Liocarpilodes* is a better fit based on *P. kauaiensis'* small size, relatively narrow carapace unadorned with large granules or spinose anterolateral teeth, weakly defined regions of the carapace, spoon-like tips of the chelae, and dactylo-propodal locking mechanism. A re-examination of the type is necessary stabilize the taxonomy of this species.

Cyclodius Dana, 1851

(see synonymy Ch. 5)

Type species. *Cyclodius ornatus* Dana, 1852 = *Cyclodius obscurus* (Hombron & Jacquinot, 1846) (by Rathbun, 1922)

Diagnosis. Carapace transversely hexagonal (Fig. 6B, C). Surface generally glabrous or with few tufts of plumose setae, smooth or granular, usually appearing smooth to naked eye, with regions well defined by deep areolas (with numerous simple, blond setae only in *Cyc. paumotensis*). Front relatively straight or sinuous; lobes separated by deep or shallow notch. Anterolateral margin with four teeth, generally without apical or accessory spines (*Cyc. paumotensis* with accessory spines). Basal antennal segment with lateral flange absent or blocking less than half length of orbital hiatus (Fig. 10B, D). Cheliped surface smooth, spinose, or granular; tips of fingers spoon-like, deeply hollowed. Ambulatory legs long or stout; tip of dactylus with distal long, pigmented spine; nonpigmented spine almost equal in length to minute. G1 tip ovate, spatulate, tubular, hooked, or adorned with numerous subdistal, straight setae, or two emergent setae (e.g., Fig. 8A, B).

Species included. *Cyclodius drachi* Guinot, 1964; *Cyc. granulatus* (Targioni-Tozzetti, 1877); *Cyc. granulosus* De Man, 1888; *Cyc. obscurus* (Hombron & Jacquinot, 1846); *Cyc. nitidus* (Dana, 1852); *Cyc. paumotensis*

(Rathbun, 1907), comb. nov.; *Cyc. sculptus* A. Milne-Edwards, 1873; *Cyc. ungulatus* (H. Milne Edwards, 1834).

Remarks. *Cyclodius* had been the subject of several revisionary works, albeit all partial (also see General Introduction). Alcock (1898: 396) gave a diagnosis of the genus and, most notably, stated that members possess carapace regions that are “well delimited and broken up into numerous convex areolae which have a smooth, bare surface.” This feature is the most conspicuous character of most *Cyclodius* species. However, as Gordon (1934: 32) pointed out, *Cyc. granulosus* and small specimens of several species have carapace granulation to varying degrees.

Recently, Ng & Yang (1998) and Clark & Ng (1999) differentiated between *Cyclodius* and other chlorodielline genera by features of the basal antennal segment, tip of the ambulatory leg dactylus, and male thoracic sternum. The latter character is difficult to use for the genera as now defined. The authors stated that *Cyclodius* has a relatively narrow sternal plastron compared to other chlorodielline genera (Ng & Yang 1998: fig. 6; Clark & Ng 1999: fig. 8). However, this feature is not clearly evident from their figures or from the examination of *Cyclodius* specimens. The only useful character of the sternal plastron appears to be the relatively longer thoracic sternite 4 of *Sulcodius*. The arrangement and length of dactylar spines on the ambulatory legs may not work. Ng and Yang (1998: 1687) characterized *Cyclodius* as having “two subdistal spines positioned side by side on the ambulatory dactylus”. They also stated that the pigmented “spine is much larger than the [subdistal] spine and is distal in position.” The problem with this character is that it varies between species, and the strength of the subdistal spines often wears with age. *Cyclodius ungulatus* and *Cyc. nitidus* possess ambulatory leg dactyli like those described and figured by Ng and Yang (1998: fig. 7B) and Clark and Ng (1999: fig. 7C). However, *Cyclodius obscurus* and *Cyc.*

granulosus are more similar to *Pilodius* or *Chlorodiella*, according to their figures and descriptions (Ng & Yang 1998: fig. 7A, C; Clark & Ng 1999: fig. 7B, D). *Cyclodius granulatus* and *Cyc. drachi* are intermediate in this dactylar character.

The utility of basal antennal segment has been questioned since Crosnier's footnote in Serène (1984) (see Remarks for *Pilodius*). *Pilodius* was characterized as possessing a basal antennal segment with a lateral flange that completely blocks the orbital hiatus despite *P. paumotensis* (= *Cyclodius paumotensis* comb. nov.) not having this trait. Instead, *Cyc. paumotensis* has an open orbital hiatus with only a slight flange (Fig. 10D). This distinction is important, as *Cyc. paumotensis* is not a typical *Cyclodius*; it does not have the typical glabrous, well-defined regions of the carapace (Fig. 6C).

The decision to place *Cyc*. *paumotensis* in *Cyclodius* is tentative. Despite being most superficially similar to species of *Soliella*, *Cyc. paumotensis* was recovered in the *Cyclodius* clade with high support in the molecular analyses (Fig. 5). Beyond strong molecular evidence, the decision was based on G1 morphology and the absence of lateral spiniform granules of the carapace, which are present in *Soliella*. The G1 of *Soliella* is conserved in the two species—i.e., narrow with a tubular spatulate or ladle-like opening and numerous stout, subdistal, proximally directed setae (Figs 8C, D) [versus broad with a wide, ovate opening, and less numerous, narrow subdistal setae, of which the most distal are not proximally directed in *Cyc. paumotensis* (Fig. 8B)]. The form of the G1 is believed to be a stronger character in classifying species, as has already been demonstrated in other studies (e.g., see Lai *et al*., 2011; Thoma *et al.*, 2014). *Cyclodius paumotensis* is also a much smaller species than *Soliella* species.

Soliella gen. nov.

Type species. *Pilodius flavus* Rathbun, 1894, by present designation.

Diagnosis. Carapace transversely hexagonal (Fig. 6D). Surface granular, covered with short, long, yellow setae; regions well defined. Front sinuous; mesial lobes arched, separated by narrow U-shaped notch; lateral lobes narrow. Anterolateral margin with four lobes tipped with emergent, anteriorly directed spine, smaller accessory spines. Basal antennal segment with lateral flange extending approximately halfway into orbital hiatus (Fig. 10F). Exterior, superior surface of chelipeds spinose, granular, with numerous long, simple, yellow setae. Ambulatory legs relatively stout; tip of dactylus with long, pigmented spine; nonpigmented, subdistal spines minute. G1 narrow, relatively straight; tip tubular or spatulate with numerous subdistal stout, proximally-directed setae (Fig. 8C, D).

Species included. *Pilodius flavus* Rathbun, 1894; *P. melanospinis* Rathbun, 1911.

Remarks. Clark & Galil (1993: 1132) synonymized *P. melanospinis* (= *Soliella melanospinis* comb. nov.) with *P. flavus* (= *Soliella flavus* comb. nov.), stating that the characters used to distinguish between the two species—i.e., areolation of the carapace, pigmentation of the chelae, and spination of the orbits—amount to "just variation." They also stated that the G1s are identical. While the external characters vary and are difficult to use for delimitation, there are clearly two distinct gonopod morphologies for the two species (Fig. 8C, D). This difference is supported by the present molecular phylogeny (Fig. 5). Therefore, the species are recognized as distinct in this study.

Members of *Soliella* gen. nov. are closest in morphology to *L. pubescens*, *L. scabriculus*, and *Cyc. paumotensis* in general shape of the carapace and especially the presence of long and short, light-colored setae (see Remarks for *Cyclodius* for comparison with *Cyc. paumotensis*). However, *Soliella* differs from *Luniella* in having a conserved G1 with a spatulate or tubular tip and a basal antennal segment with an anterolateral flange that reaches less than halfway into the orbital hiatus (Figs 8C, D, 10F) (versus a G1 with a flattened, sickle-shaped tip and flange of the basal antennal segment completely blocking the orbital hiatus in *Luniella*) (Figs 9C, D, 10E).

Etymology. The genus name is derived from a combination of the Latin word for sun, 'sol', and the last five letters of the subfamilies' type genus, *Chlorodiella*. 'Sol' alludes to the blond or golden setae on the surface of the carapace of these crabs.

Luniella gen. nov.

Type species*. Pilodius pugil* Dana, 1852, by present designation.

Diagnosis. Carapace transversely hexagonal (Fig. 6E). Surface granular, glabrous, or with numerous short yellow setae and scattered long setae. Front with broad, arched mesial lobes separated by shallow or deep median notch; lateral lobes narrow. Anterolateral margin with 4 spinose teeth, few or no accessory teeth. Basal antennal segment with lateral flange generally completely blocking orbital hiatus, excluding flagellum (Fig. 10E). External, superior surfaces of chelipeds granular and/or spinose; glabrous or setose. Ambulatory legs granular or smooth, with numerous setae sometimes restricted to extensor margin; tip of dactylus with long, pigmented spine; nonpigmented subdistal spines minute. G1 tip flatted, sickle-like or twisted (Fig. 9C, D).

Species included. *Pilodius pubescens* Dana, 1852; *Pilodius pugil* Dana, 1852; *Pilodius scabriculus* Dana, 1852; *Pilodius spinipes* Dana, 1852.

Remarks. *Luniella* is most readily distinguished from other chlorodielline (*s. str.*) species by its unique sickle-shaped G1 tip. This feature is conserved even when it is longitudinally twisted, like in *L. scabriculus* (Fig. 9C). With the exception of *L. scabriculus,* all of the members of *Luniella* have an orbital hiatus that is completely blocked by the anterolateral flange of the basal antennal segment, a feature that it shares with *Pilodius*. In *L. scabriculus*, this character varies. However, most large specimens possess a basal antennal segment that extends more than halfway into the orbital hiatus. See Remarks for *Luniella*, *Cyclodius*, and *Pilodius* for further comparisons.

Etymology. The genus name is derived from a combination of the Latin word for moon, 'luna', and the last five letters of the subfamilies' type genus, *Chlorodiella*. 'Luna' alludes to the sickle moon-shaped tip of the G1 of these crabs.

Discussion

The decision to restrict Chlorodiellinae to *Chlorodiella*, *Cyclodius*, *Pilodius*, *Luniella* gen. nov., and *Soliella* gen. nov., while provisionally transferring the other genera to *incertae sedis* was made with some hesitation. Given the high support for the new chlorodielline clade and cohesive morphology of this group to the exclusion of the removed genera, it was clear that these genera had to be withdrawn (Fig. 5). The problem, then, was the unresolved state of the many xanthid subfamilial boundaries, obvious in the molecular analysis with Etisinae, and several other subfamilies, divided and scattered throughout the xanthid phylogeny. There were two options: treat *Tweedieia*, *Ratha*, *Sulcodius*, *Vellodius*, and *Liocarpilodes* as *incertae sedis*, or place them tentatively in other subfamilies. The former was chosen as a compromise solution and in concordance with the constrained topology test.

The topology of the present xanthid tree indicates a monophyletic Chlorodiellinae, including *Pilodius*, *Cyclodius*, *Chlorodiella*, *Soliella*, gen. nov., and *Luniella*, gen. nov., but excluding *Liocarpilodes*, *Ratha*, *Sulcodius*, *Tweedieia*, and *Vellodius* (Fig. 5). Two characters, spoon-like tips of the fingers of the claws and a dactylo-propodal locking mechanism on the walking legs, have historically been used to unite members of Chlorodiellinae and Etisinae. However, the utility of these supposedly diagnostic features was called into question recently (Lai *et al.*, 2011; Ng *et al*., 2008). The present phylogenetic analyses indicate that these characters are indeed paraphyletic and have evolved independently in different lineages. The Chlorodiellinae is redefined here and delimited based on a new suite of characters.

The genus *Liocarpilodes* is clearly polyphyletic, with members segregating into three clades that possess strikingly different morphological features used in xanthid taxonomy to define genera—e.g., characteristics of the male abdomen, thoracic sternum, and G1; spination of the chelipeds; morphology of the tip of the ambulatory dactylus; and morphology of the anterolateral margin of the carapace. Based on the phylogeny, *L. integerrimus* is allied with *Etisus bifrontalis*, *E. odhneri*, *E. demani*, and *E. albus* (*Etisus* 4) with moderate support (pP = .97, ML BS = 54, not recovered in MP). *Liocarpilodes armiger* and *L. pacificus* are well-supported (pP = 1, ML BS = 100, MP BS = 100) sister species, but their relationship with other xanthid genera is not resolved. The same is true for *L. harmsi.* The only *Liocarpilodes* species not included was *L. biunguis*. Given the almost indistinguishable G1s, and similar sterna and abdomen, *L. biunguis* is likely allied with *L. harmsi*. Further commentary is beyond the scope of this study, except to say that *Liocarpilodes* likely comprises three genera and is in need of taxonomic revision.

Etisinae, as currently defined (Ng *et al*., 2008), comprises only two genera: *Etisus* and the monotypic *Paretisus* Ward, 1933. However, the topology of the xanthid phylogeny indicates that *Etisus* represents at least three independent lineages (Results; see also Lai *et al.*, 2011: 434), each defined by suites of uniting morphological characters. The members of *Etisus* 2 that were sampled for the analyses have a well-developed dactylo-propodal locking mechanism and a strikingly long male thoracic sternum (Fig. 7E). *Etisus* 3 specimens are united by their reduced dactylo-propodal locking mechanism and comparatively shorter, broader male thoracic sternum (Fig. 7F). These features vary or are unknown in *Etisus* 4, but members of the clade are united by a conserved G1 morphology—i.e., long and narrow, without stout, long distal setae. In summary, the Etisinae, as presently defined, is also in need of revisionary work and likely comprises several genera.

These taxa have historically been associated with the Chlorodiellinae, but there placement now is uncertain. The type species of *Liocarpilodes*, *L. integerrimus*, was recovered with *Etisus* 4 (pP = 0.97, ML BS < 70), so the genus may end up in Etisinae pending necessary revisions of *Liocarpilodes* and Etisinae. *Vellodius* and *Sulcodius* grouped with *Etisus* 2 and *Etisus* 1, respectively, in the combined BI analysis, albeit with low support. Based on these data and the taxa's similar transversely hexagonal carapaces, spoon-like tips of the chelae, and dactylo-propodal locking mechanisms on the ambulatory legs, these genera are probably close to *Etisus s. lat.* Greater taxon sampling of Etisinae for morphological comparisons (e.g., investigating male sternal and male gonopod characters) and molecular phylogenetics will undoubtedly be necessary and insightful. The same is true of *Tweedieia*.

CHAPTER 4.

A NEW GENUS FOR *CHLORODIELLA LONGIMANA* (H. MILNE EDWARDS, 1834) SUPPORTED BY MORPHOLOGY AND MOLECULAR DATA

Introduction

Chlorodiella longimana (H. Milne Edwards, 1834) is restricted to the tropical and subtropical western Atlantic Ocean where it is found inhabiting rocky shores and coral reef areas but at much lower densities than most allied taxa (Abele 1976). The confusing taxonomic history of chlorodielline-associated genera combined with *Chlorodiella longimana'*s atypical western Atlantic Ocean distribution led to the investigation of the group to determine what, if any, relationship exists between *Cyc. longimana* and the rest of Chlorodiellinae. Attempts to locate the holotype of *Cyc. longimana* at the Muséum National d'Histoire Naturelle in Paris have proven unsuccessful, and it is believed that the type is no longer extant. As a result, it is necessary to establish a neotype in an effort to stabilize the species. This work shows that *Cyc. longimana* belongs to an undescribed genus that falls outside the Chlorodiellinae. The description and discussion for this new genus has been published in Lasley *et al.* (2013), which was done during the period of the present dissertation.

Systematic account

Family Xanthidae MacLeay, 1838

Subfamily Chlorodiellinae Ng & Holthuis, 2007

Ratha Lasley, Lai & Thoma, 2013.

(Figs 11–13)

Ratha Lasley, Lai & Thoma 2013: 380

Type species. *Chlorodius longimanus* H. Milne Edwards, 1834: 401, by original designation

Diagnosis. Carapace (Fig. 11A, B) transversely hexagonal. Surface convex, covered with minute granules, appearing smooth without magnification. Regions weakly defined, without distinct areolas. Front (Fig. 11C) about one-third width of carapace, double rimmed. Anterolateral margin with four teeth excluding exorbital tooth. Antennules folded obliquely. Orbits relatively small. Basal antennal segment (Fig. 12B) with lateral flange elongated, reaching almost halfway into orbital hiatus, flagellum excluded from orbit. Endostome minutely granular, without longitudinal branchial ridges. Third maxilliped (Fig. 12C) endopod merus subquadrate, anterior margin slightly convex, expanded laterally, with medial indention, concave junction with carpus. Chelipeds (Figs 11E, F, 12A) subequal, long, length from basis to distal margin of merus about equal to carapace length. Anterior margin of merus with large, acute teeth. Fingers black, lined with tufts of setae on flexor surface of cutting margin, tips white, spoon-like, hollowed, each with brush of setae behind edge. Ambulatory legs moderately long, stout, setose; dorsal margin lined with spines; dactylo-propodal locking mechanism well

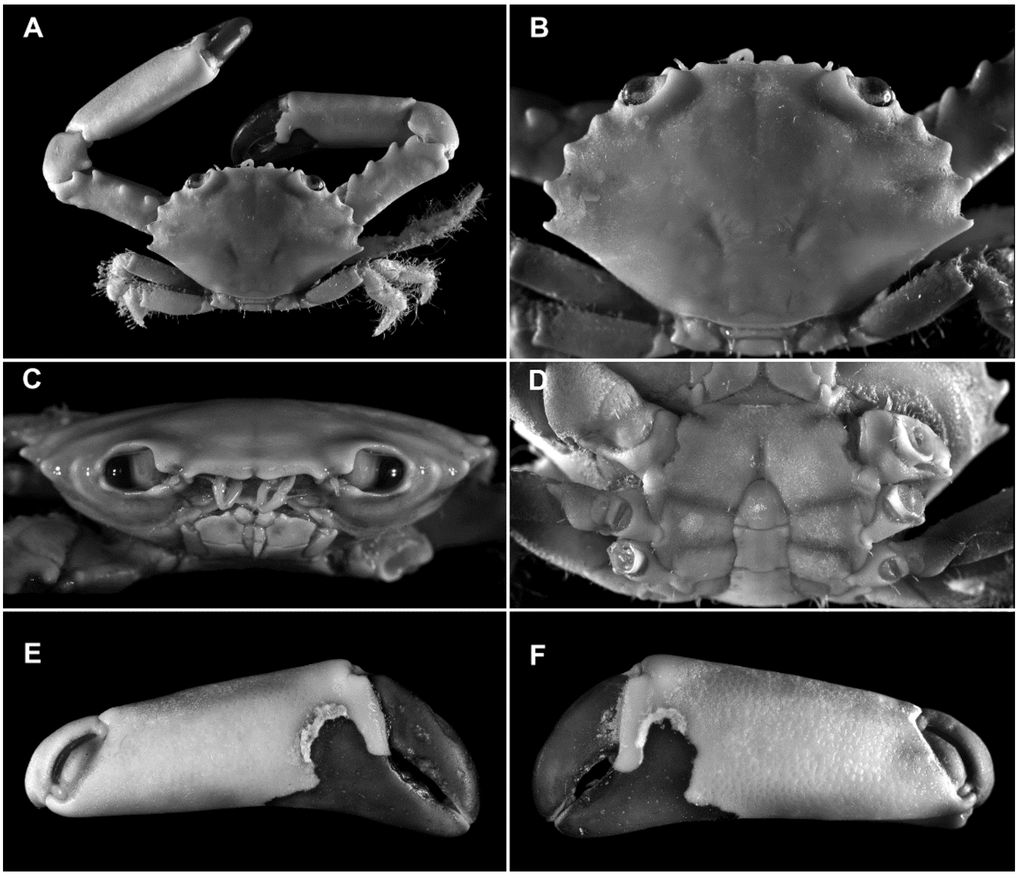

Figure 11. *Ratha longimana*, Lasley, Lai & Thoma, 2013, neotype male, 20.3_12.7 (USNM 1190165), Trinidad; A, carapace, dorsal view; B, dorsal view; C, frontal view; D, thoracic sternum; E, minor chela, external view; F, major chela, external view.

developed. Male abdomen (Figs 11D, 13B) long, narrow, with somites 3–5 appearing indistinguishably fused externally, appearing smooth to naked eye; somite 3 not forming a locking system with thoracic episternite 7; telson subtriangular, longer than broad, tip rounded, anteriorly reaching sternal condyle of first ambulatory leg. Male thoracic sternum (Fig. 11D) broad, granulate; episternites not delimited by a sulcus; sternites 2, 3 flat; press-button on sternite 5 near suture between sternites 5 and 6. G1 (Fig. 13C, D) moderately stout, laterally flattened; apex acute, curved laterally. Second gonopod (Fig. 13E) less than 1/3 length of first. Vulva of mature females circular, large, in middle of sternite 6; aperture opens medially.

Etymology. The genus is named after the American carcinologist Mary Rathbun, in honour of her exemplary contributions to brachyuran taxonomy. The name is arbitrarily derived from the first four letters of her family name. Gender feminine.

Assigned Species. *Chlorodius longimanus* H. Milne Edwards, 1834.

Remarks. *Ratha* Lasley, Lai & Thoma 2013, differs from the chlorodielline genera, *Cyclodius*, *Pilodius*, *Soliella, Luniella* and *Chlorodiella*, by having a smooth, unadorned carapace, with only slightly raised, indistinctly defined regions (Fig. 11A, B) (vs. raised, distinct regions often adorned with setae and/or granules in all chlorodielline genera except *Chlorodiella*). *Garthiella* was recently revised by Mendoza & Manuel-Santos (2012), who also removed the genus to its own subfamily, Garthiellinae Mendoza & Manuel-Santos, 2012. The genus is significantly different from all other chlorodiellines in any case (see Mendoza & Manuel-Santos, 2012), so there is no need to comment further. In comparison to *Liocarpilodes*, *Ratha* has a relatively straighter anterolateral margin, a relatively wide front, and a G1 with short, stout, and downward pointing distal setae (Figs 11A, C, 13C, D) (vs. a rounded anterolateral margin, a narrower front, and a G1 with long, fine subapical setae) (Serène 1984: 261, pls 37A–D, figs 174–177. In the general appearance of the carapace and chelae, *Ratha* is most similar to *Chlorodiella*. It differs in having ambulatory legs with dactyli ending in a single tip and relatively narrower orbits (Figs 11A, C, 13A) (vs. bifid dactyli and wider orbits in *Chlorodiella*) (see Ng & Yang 1998: figs 5a, 7a; Serène 1984: pl. 36).

The only other Western Atlantic Ocean genus similar in morphology to *Ratha* is *Paraliomera* Rathbun, 1930 (Liomerinae). Both genera have a transversely ovate, smooth carapace with regions barely marked and chelae with similar spoon-like tips. *Ratha*, however, possesses a relatively narrower carapace, distinctly acute anterolateral teeth, and subequal chelipeds (Fig. 11A, E, F) (vs. a broad carapace, an obscurely lobed or toothed anterolateral margin, and very unequal chelipeds in *Paraliomera*) (Rathbun 1930: 243, pl. 101, figs 1–5).

Ratha longimana (H. Milne Edwards, 1834).

(Figs 11–13)

Chlorodius longimanus H. Milne Edwards 1834: 401. — Desbonne & Schramm 1867:30.

Chlorodiella longimanus, Rathbun 1897b: 14.

Chlorodiella longimana, Rathbun 1900: 288; 1901: 36; 1930: 462, pl. 186; 1933: 68, fig. 58. — Rodriguez 1959: 269, 275. — Garth 1978: 320, 326. — Lemaitre 1981: 250. — Keith 1985: 265, fig. 7E. — Abele & Kim 1986: 48, 186. — Camp *et al*. 1998: 148. — Álvarez *et al.* 1999: 12. — Tagliafico *et al.* 2005: 93. — Ng *et al.* 2008: 234. — Felder *et al*. 2009: 1084.

Ratha longimana, Lasley, Lai & Thoma 2013: 386

Material Examined. Neotype male, 20.3 × 12.7 mm (USNM 1190165), under rocks and in crevices in coral heads, Cumana Bay, Trinidad, Caribbean Sea, coll. J. Stanley, 6 January 1970. — 1 male, 12.8 × 7.9 mm (ULLZ 12144), amongst rubble, CSN-12144, rubble, Stn. 2, Bocos del Torro, Caribbean, Panama, coll. D. Felder, 8 August 2004. — 1 male, 16.6 × 10.1 mm, 1 ovig. female, 13.3 × 8.3 mm, 2 females, 14.2 × 9.0 mm, 9.8 × 6.2 mm (USNM 139255), under rocks and in crevices in coral heads, Cumana Bay, Trinidad, Caribbean Sea, coll. J. Stanley, 6 January 1970. — 1 ovig. female, 15.2 × 9.2 mm (ULLZ 11098), Isla Enmedio, CSN-11098, Veracruz, Mexico, coll. J. Rickner, 1973. — 1 female, 16.2 × 9.8 mm (ULLZ 11247), Isla Lobos,

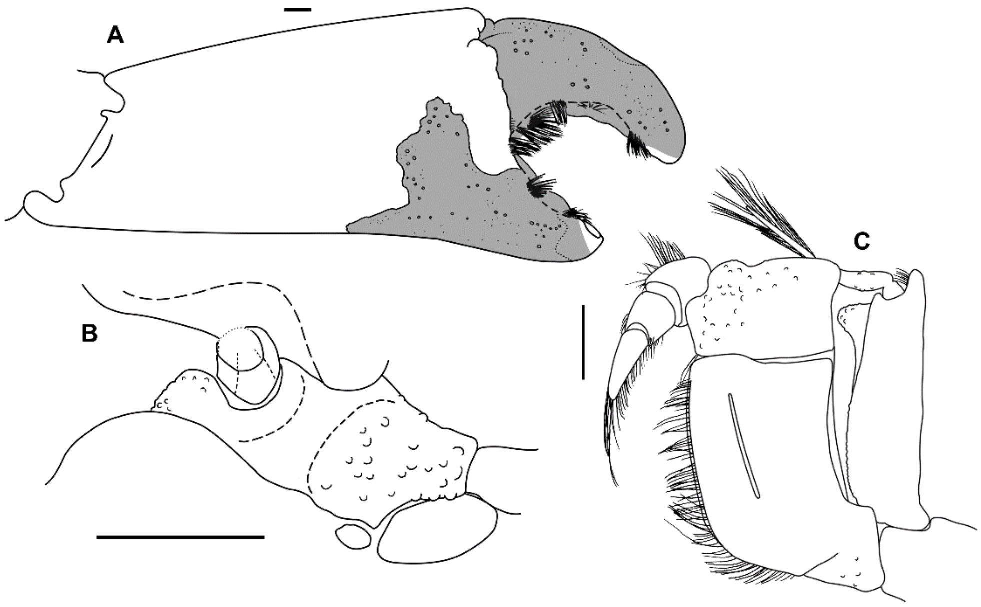

Figure 12. *Ratha longimana*, comb. nov., neotype male, 20.3_12.7 (USNM 1190165), Trindad; A, major chela, internal view; B, right basal antennal segment, frontal view; C, left third maxilliped, extermal view. Scales:
1.0 mm.

CSN-11247, STN I-4-2, Veracruz, Mexico, coll. J. Rickner. — 1 male, (UF 32481), in dead *Acropora*, reef, 4–5 meters depth, Pinel Island, Saint Martin, Caribbean Sea, coll. A. Anker, J. F. Maréchal, 24 April 2012.

Redescription. Carapace (Fig. 11A) transversely hexagonal, about 1.7 times broad as long. Surface convex, covered with minute granules, appearing smooth without magnification. Front (Fig. 11C) about one-third width of carapace, double rimmed; upper rim straight; lower rim sinuous joining mesially to form V-shaped notch, separated from orbit by sulcus. Regions weakly defined; 1M slightly raised; anterior of 2M joining with 2L and 3L; 2L and 3L forming transverse ridge, separated from orbit and posterior regions by transverse troughs; posterolateral border of 3M indicated with longitudinal furrows. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low, obtuse, rounded; tooth 2 higher, subacute; teeth 3 and 4 acute, anteriorly directed; tooth 3 largest, most prominent.

Eyestalk minutely granulate. Orbit about 0.13 width of carapace at widest point from anterior view; superior margin with slight medial and medio-lateral transverse sulci; inner supraorbital tooth separated from front by broad sulcus; outer supraorbital tooth separated from outer suborbital tooth by V-shaped notch; inferior margin concave, granulate; mesial and lateral suborbital teeth projecting anteriorly, rounded, inner suborbital tooth lamelliform.

Antennules folded obliquely. Basal antennal segment (Fig. 12B) with anterolateral angle slightly expanded, reaching almost halfway into orbital hiatus, flagellum excluded from orbit.

Epistome surface minutely granulate, anterolateral margin meeting nephridiopore operculum, posterolateral margin overlaid by pointed, granular pterygostomial projection. Endostome without longitudinal ridges. Third maxilliped (Fig. 12C) exopod moderately stout, microscopically punctate, without setae except at junction with flagellum; endopod with ischium stout, about 0.7 times wide as long (medial width by medial length), longitudinal sulcus near extensor margin, extensor margin thin with fringe of setae; merus subquadrate, anterior margin expanded laterally, with distinct indentation or median notch, rounded convexly towards concave junction with carpus.

Chelipeds (Figs 11E, F, 12A) subequal, long, length from basis to distal margin of merus about equal to carapace length. Anterior margin of merus with 4 large, acute, laterally directed teeth. Propodus smooth, long, tip of fixed finger to ventral junction with carpus about 1.5 times length of merus. Fingers black, surface minutely punctate; tips white, hollowed, spoon-like, with subapical brush of setae on cutting edge; immovable finger with denser brush of setae, smaller patch of setae on flexor surface of cutting margin, black pigment extending 2\5 length of lower margin. Dactylus with about four densely packed brushes of setae proximally on flexor surface of cutting margin, one sparse patch of setae on flexor surface of cutting margin midway to tip. Major chela more robust, with denser, more numerous patches of setae, movable finger more concave, otherwise similar to minor chela.

Ambulatory legs (Figs 11B, 13A) moderately long, stout, setose; extensor surface sparsely covered with robust plumose setae, lined with sharp, arched spines, arranged in 2 rows on carpus and propodus; merus of last leg not reaching last anterolateral tooth when apposed against carapace; dactylo-propodal locking mechanism well developed, formed by lamellar extension of distal margin of propodus that slides beneath a bulbous flange on dactylus; tip of dactylus with single terminal spine and 2 slightly enlarged, downward-pointing, subdistal spines.

Male abdomen (Figs 11D, 13B) long, narrow, with somites 3–5 fused, appearing smooth to naked eye but minutely granulate; somites 1 and 2 with margins granulate, sutures between somites 3–5, evident as slight lateral indentions, somite 3 not locking with thoracic episternite 7; somite 6 broadest distally, greatest width about equal to length, appearing longer due to concave lateral margins. Telson subtriangular, longer than broad, tip rounded, reaching sternal condyle of first walking leg.

Male thoracic sternum (Fig. 11D) broad, granulate; sternites 2 and 3 flat; suture between sternites 1 and 2 indicated by row of few long, stout, simple setae; suture between sternites 3 and 4 evident as short transverse lateral sulci. Press-button on sternite 5 near suture between sternites 5 and 6. Sternite 7 not divided by transverse sulcus near sternal condyle of third ambulatory leg. Opening for male papilla large, elliptical, located on fifth pereopod coxa, just anterolateral to sternal condyle, covered by lateral lobe of third abdominal segment.

G1 (Fig. 13C, D) moderately stout, laterally compressed, pointed; sternal and abdominal margins lined with short, stout setae; distal 1/5 with

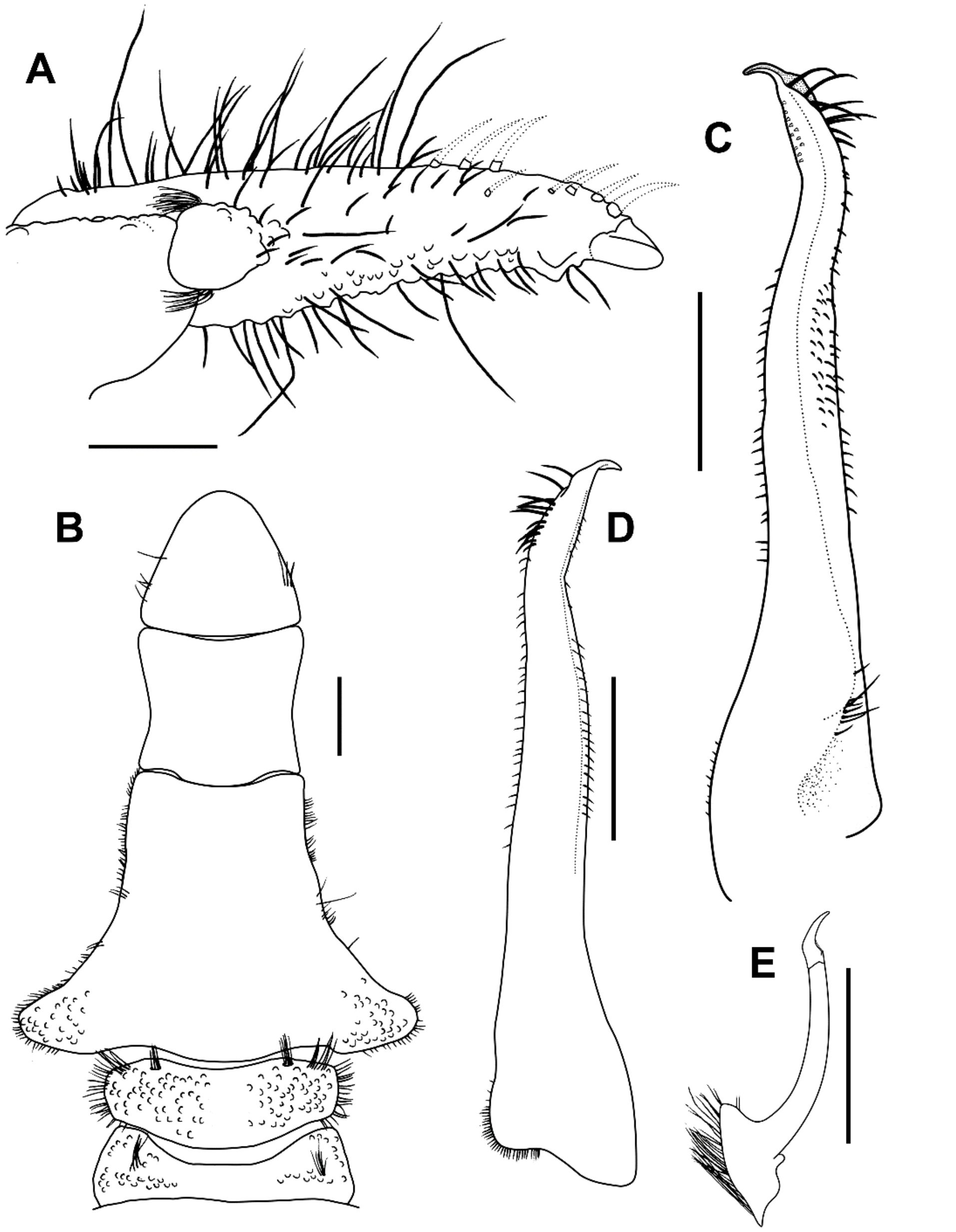

Figure 13. *Ratha longimana*, Lasley, Lai & Thoma, 2013, 20.3_12.7 (USNM 1190165), Trinidad; A, right fourth ambulatory leg; B, male abdomen, external view; C, right G1, external view; D, right G1, internal; E, G2.

abdomino-medial surface having array of short spines; lateral surface excavate appearing longitudinally hollowed with about 8 mixed-length subdistal setae; apex lamelliform, strongly deflected mesially. G2 (Fig. 13E) less than 1/3 length of first gonopod, terminating in long, slender spine.

Live Coloration. Coloration entirely brown with minute light-blue spots, more numerous on thoracic sternum, third maxillipeds, ambulatory legs.

Variations. Adult female specimens conform closely to the morphology of the male holotype, excluding sexual structures. Female abdomen appears as an elongate oval from second somite to telson. Vulva of mature females are located on sternite 6 and are circular, moderate in size and positioned slightly closer to the suture between sternites 5 and 6 than 6 and 7. The aperture of the gonopore is wide, almost completely the circumference of the vulva, and the membrane is restricted to the lateral margin, covering less than 1/4 the diameter of the aperture.

Smaller specimens tend to have more defined anterolateral transverse ridges and the anterior borders of regions 1M, 2M and 3M are more defined, although some large specimens have relatively well defined regions. Also, the anterolateral teeth of the carapace and the spines of the merus of the chelipeds are sharper with corneous tips in small specimens. Furthermore, in smaller specimens the frontal rim is often distinctly serrated, and the apex of the male G1 is not as strongly deflected mesially.

Distribution. *Ratha longimana* is recorded from the north coast of Brazil, the western coast of the Gulf of Mexico, southern Florida, and throughout the Caribbean. It was reported from St. Thomas Island, West Africa by Osorio (1887) but no specimens have been collected in the region since. Monod (1956) first cast doubt on the veracity of Osorio's record, followed by Manning and Holthuis (1981), who believed that Osorio's record was based on either misidentification or erroneously labelled specimens. Hence, the eastern Atlantic Ocean is considered extralimital for this species.

Habitat. This species is known from habitats with hard substrates such as rocky areas, coral reefs, rubble, and clumps of calcareous algae from shallow waters to 154 meters (see Lemaitre 1981, Abele 1976).

Type Status. Henri Milne Edwards (1834) apparently described the species from only one male specimen, as he gives a description of the male chelipeds and lists just one measurement: length = 6 linges (ca. 13.5 mm). A search for the holotype in the collections of the Muséum National d'Histoire Naturelle in Paris, France by Peter Castro was unsuccessful, and the type specimen is presumed to be lost. Although the authors were unable to locate material from Puerto Rico, the type locality, a large male in good condition from Cumana Bay, Trinidad (roughly 600 miles SE of Puerto Rico), was found in the crustacean collection of the National Museum of Natural History (USNM), Washington D.C., USA. Given the scarcity of available specimens in good condition, the relative proximity of Trinidad to the type locality, and the need to stabilize the species, this specimen was designated as the neotype (USNM 1190165) by Lasley *et al*. (2012).

Remarks. Since its description by H. Milne Edwards (1834), the species now treated as *Ratha longimana* comb. nov., has had a relatively stable taxonomic history. Much of this is likely due to there being no other Western Atlantic Ocean species with a similar habitus. Of Western Atlantic Ocean species, *Ratha longimana* is morphologically most similar to *Paraliomera dispar* (Stimpson, 1871), with both species having chelae with spoon-like tips and a transversely-ovate, smooth carapace with barely marked regions. However, *Ratha longimana* comb. nov., has a proportionately broader carapace with lateral transverse ridges and acute teeth on the anterolateral margin (Fig. 11A) (vs. narrower with no ridges and an obscurely lobed anterolateral margin) (Rathbun 1930: 244, fig. 4). Although the chelipeds of both species are somewhat spoon-like at the tips, those of *P*. *dispar* are extremely unequal, whereas those of *R. longimana* are subequal.

Discussion

Based on the topology of the xanthid tree, the decision to designate a new genus for *Chlorodiella longimana* and remove it from the Chlorodiellinae is well supported (Fig. 5). Morphologically, however, *Ratha* Lasley *et al*., 2013, possesses diagnostic characteristics representative of Chlorodiellinae Ng & Holthuis, 2007: spoon-tipped chelae; a relatively broad, distinctly chlorodielline-like, transversely-ovate carapace; a broad, hardly-projecting front; and a well-defined ambulatory dactylo-propodal locking mechanism (Figs 11, 13A). It also possesses features of the thoracic sternum and abdomen recently shown to be characteristic of the *Chlorodiella-Pilodius-Cyclodius-Luniella-Soliella* group: flat thoracic sternites 2 and 3, no division of sternite 7 near the sternal condyle of the third ambulatory leg, somite 3 of the abdomen not locking with thoracic episternite 7, and the tip of the male telson reaching the sternal condyle of the first walking leg (Figs 11D, 13B) (Lai *et al.* 2011). *Ratha*, however, does not possess the typical bifid dactylus, which was tenuously used to characterize Chlorodiellinae (Fig. 13A) (Clark & Ng 1999: 357; Ng & Yang 1998: 1687); although this feature is not present in *Cyclodius* Dana, 1851 either. *Ratha* has a single distal dactylar spine with two slightly enlarged, downward-pointing, subdistal spines (see Clark & Ng 1999: fig. 7c, Ng and Yang 1998: fig. 7b).

Ratha is also interesting as although it falls outside the Chlorodiellinae, its position in the Xanthidae is less clear (Fig. 5). Lai et al. (2011) (see also Thoma et al., 2013) showed that many eastern American xanthid genera now classified in the Euxanthinae, Actaeinae and Zosiminae actually form natural groups and *Ratha* is probably in this same situation. This “east American clade” will need to be looked at in greater detail to see if they can also be supported by morphological characters.

CHAPTER 5.

INTEGRATIVE TAXONOMIC REVISION OF THE SUBFAMILY CHLORODIELLINAE

Introduction

Taxonomists have described around 1.7 million species in the past 250 years, give or take 1 or 2 hundred thousand (Hawksworth & Kalin-Arroyo 1995, Tangley 1997, The World Conservation Union 2010). The number is impressive, especially when considering most of these were described solely using morphology. However, according the most recent estimates, the ocean alone likely houses around 0.3 to 2.2 million species, of which only 0.25 million have been described (Mora *et al*. 2011, Appletans *et al*. 2012, Costello *et al*. 2012). Meanwhile, anthropogenic degradation is causing alarming defaunation in the ocean (McCauley *et al*. 2015). Given this pressure and the fact that taxonomy is the baseline for conservation studies, describing and classifying the immense number of unknown species is imperative.

DNA barcodes are valuable tools for identifying potential new species. However, there has been considerable controversy on the efficacy of species delineation via barcoding (Goldstein & DeSalle 2010). One of the early oversights of the barcoding movement involved the use of thresholds. Hebert *et al*. (2003) proposed to identify species based on a fixed percent difference (3% in their case) in COXI sequences. From this widely cited paper, the use of barcoding thresholds grew from identification to delineation (Stoeckle 2003, Hebert 2004). The use of a threshold relies on there being a gap between interpecific distance and intraspecific variation. However, this “barcoding gap” is not always present between species—i.e., interspecific distance is sometimes less than intraspecific variation (Meyer & Paulay 2005). Furthermore, the use of mean interspecific distance has been widely used, despite artificially inflating the barcoding gap (Meier *et al*. 2008), and several other methodological and evolutionary problems with DNA barcodes have arisen (see Ch. 1 Introduction). Given these problems, proper analyses of DNA barcodes combined with other sources of data (i.e., integrative taxonomy) are important for species delineation.

A third consideration in species delineation is deciding which of the over 20 species concepts to apply. This is particularly important, as the application of different concepts can result in different numbers of delineated species (Laamanen *et al*. 2003, Tan *et al*. 2008, Schwentner *et al*. 2011) (see Chapter 1). Despite all of the challenges, integrating and analyzing DNA sequence and morphological data correctly, and specifying a species concept clearly, can result in discovery of historical processes leading to speciation and proper delineation, even in taxa where taxonomic problems abound.

Chlorodielline crabs are some of the most abundant crustaceans inhabiting coral reef environments in the Indo-West Pacific region (Peyrot-Clausade 1977, 1979; Plaissance *et al*. 2011; Leray *et al*. 2012; Lasley *et al*. 2013; Lasley *et al*. 2015). Yet despite their ubiquity, the taxonomy of the group is in serious need of revision. Recent studies have done substantial work on the group at a subfamilial and generic level (Lai *et al*. 2011, Lasley *et al*. 2013, Lasley *et al*. 2015). However, species-level taxonomy of Chlorodiellinae is still in need of work.

Serène (1984) was the last authority to review Chlorodiellinae as a whole. His monograph of Indian Ocean xanthoid crabs laid a solid foundation, treating each species with diagnoses, keys for identification, and informative figures and photographic plates. However, the generic taxonomy has been completely reworked since Serène's (1984) publication due polyphyly of the genera (Lasley *et al*. 2015). Furthermore, the taxonomic status of several species treated by Serène is questionable. For example, two "forms" of *Chlorodiella laevissima* were designated: *C. laevissima* form "robusta" and *C. laevissima* form "laevissima". Also, several specimens of *Luniella* were designated as *Pilodius* aff. *spinipes* (= *L.* aff. *spinipes*). Additionally, six species have been described since Serène's (1984) study, and were therefore not treated: *Chl. crispipleopa* Dai, Yang, Song & Chen, 1986; *Chl. quadrilobata* Dai, Cai & Yang, 1996; *Chl. spinimera* Dai, Cai & Yang, 1996; *Pilodius cephalalgicus* Clark & Galil, 1993; *P. concors* Clark & Galil, 1993; and *P. moranti* Clark & Galil 1993.

Subsequent to Serène's (1984) work, several studies have treated Chlorodiellinae piecemeal. For example, Dai, Yang, Song & Chen (1986) treated the subfamily in their volume of crabs from the "China Seas". However, only 20 chlorodielline species were covered and two other subfamilies, Etisinae Ortmann, 1893 and Cymoinae Alcock, 1898, were included with Chlorodiellinae under the junior synonym Chlorodinae Alcock, 1898. They also described a new species, *Chl. crispipleopa*, which as it turns out, is conspecific with *Chl. cytherea* (see taxonomic account below). Another partial treatment of the subfamily was Clark & Galil's (1993) thorough revision of *Pilodius*. Unfortunately, the key to species is problematic (personal observation). This may be due to the fact that *Pilodius*, as was defined, comprised two additional genera: *Luniella* and *Soliella* (Lasley *et al*. 2015). Also, the characters used to differentiate the three conspecific taxa *P. concors*, *P. pilumnoides*, and *P. cephalalgicus* vary with size of the specimens (see results and taxonomic accounts). Furthermore, the synonymy of *P. philippinensis* (Ward, 1936) with *P. granulatus* Stimpson, 1858 was later overturned (Davie 2005), and other synonymies are in need of further study and elaboration (e.g., *Soliella flava* and *S. melanospinis*).

Ng *et al.* (2008), recognized eight chlorodielline genera: *Chlorodiella* Rathbun, 1897; *Cyclodius* Dana, 1851; *Pilodius* Dana, 1851; *Garthiella* Titgen, 1986; *Liocarpilodes* Klunzinger, 1913; *Sulcodius* Clark & Ng, 1999; *Tweedieia* Ward, 1934; and *Vellodius* Ng & Yang, 1998. The latter five were subsequently removed from Chlorodiellinae (Mendoza & Manuel-Santos 2012, Lasley *et al*. 2015). The remaining three were redefined and their species were divided into the five current chlorodielline genera: *Pilodius*, *Cyclodius*, *Chlorodiella*, *Luniella* Lasley, Klaus & Ng, 2015, and *Soliella* Lasley, Klaus & Ng, 2015. All species recorded in Ng *et al*. (2008) are in current use except *Cyc. maculatus* (Stimpson, 1860). *Cyclodius maculatus* was listed in two genera in Ng *et al.* (2008), *Etisus* H. Milne Edwards, 1834 and *Cyclodius*. It belongs in *Etisus* (Lasley *et al*. 2015). Given these taxonomic changes, there are 35 currently recognized species of Chlorodiellinae.

As reflected in many of these revisionary works, male gonopods (G1s) are important for identification of xanthids (Guinot 1968). They have been relied upon extensively for chlorodielline species diagnosis and delineation (e.g., Serène 1984; Serène & Nguyen 1959, 1969; Dai & Yang 1991; Clark & Galil 1993). Importantly, many arthropod species are distinguished via genitalic features which have been used to infer reproductive isolation (e.g., Schwentner *et al*. 2011).

In this study, the species-level taxonomy of the Chlorodiellinae is revised via the integration of G1 and other morphological characters, and molecular phylogenetics. Reproductive isolation is used as a criterion for delineating species. Gene trees for each genus (*Chlorodiella*, *Cyclodius*, *Pilodius*, *Luniella*, and *Soliella*) using 894 COXI sequences are presented and compared with species designations based on G1 morphology. Uncorrected p distances are used to explore the data for barcoding gaps. Species are also clustered using SpeciesIdentifier from the TaxonDNA version 1.6.2 package (Meyer *et* al. 2006). For each species, members of major subclades in the ML and BI COXI trees were sequenced for 16S rRNA gene, 12S rRNA gene, and H3. The resulting phylogeny of the Chlorodiellinae is also presented. Keys, diagnoses and figures for all species are provided. The utility of using distinct G1 morphology as a proxy for species delineation is tested against current taxonomy based on G1 and external morphology, monophyly of the combined dataset, reciprocal monophyly of the COXI genetrees, presence of a barcoding gap, and SpeciesIdentifier cluster analysis.

Material and Methods

Taxon Sampling and Morphological Identification

All of the 35 chlorodielline species were included in the morphological examination except *Chlorodiella quadrilobata* Dai, Cai, &Yang, 1996, *Chl. ohshimai* Miyake & Takeda, 1967, *Cyclodius perlatus* Nobili, 1905, and *Pilodius kauaiensis* Edmondson, 1962. These are obscure species of questionable status which have only been recorded in original descriptions (see taxonomic accounts). Of these 31 remaining species, sequence data was obtained from all except *Cyc. drachi* Guinot, 1964. The 30 species with morphological and molecular data available for this study are included in Table 1. Identifications were largely made via the keys and diagnoses from Forest and Guinot (1962), Guinot (1964), Serène (1984), Dai and Yang (1991), and Clark and Galil (1993). Representatives of each G1 morphotype were selected for scanning electron microscopy. Techniques for preparation and SEM imaging followed Lasley *et al.* (2015). Eight hundred ninety-four specimens were selected for the molecular analyses. Sequences were generated de novo for this study or provided by the Moorea Biocode Project, Indonesia Biodiversity Research Center, or the Florida Museum of Natural History's Division of Invertebrates (SM 2).

Analyses

A total of 894 COXI, 38 12S rRNA, 39 16S rRNA, and 37 H3 sequences were used for the analyses (SM 4, 6). Sequences were generated and aligned following Lasley *et al*. (2015) (Chapter 3). Phylogenetic trees were inferred from the concatenated dataset using maximum-likelihood (ML), maximum parsimony (MP) and Bayesian Inference (BI) methods using the same methods in Lasley *et al*. (2015) (Chapter 3). The same methods used for the concatenated dataset were used for the BI and ML COXI trees. Uncorrected p distances for determining interspecific smallest distances and intraspecific variation were calculated with MEGA 6 (Kimura 1980, Tamura *et al*. 2013). Each genus was analyzed with a 3% threshold in the "cluster" module of SpeciesIdentifier. Other thresholds were iteratively tested.

Results

Morphological Examination

Twenty-seven G1 morphologies were examined (Pls 37–45). Most of these directly corresponded with described species listed in Ng *et al*. 2008—i.e., one G1 morphology matching one described species. However, this one to one relationship did not always hold. Specimens of *Chlorodiella laevissima*

(Dana 1852) had three distinct G1 morphologies (Pls 38C, D, 39A). Specimens of *Pilodius pilumnoides* (White, 1848), *P. concors* Clark & Galil 1993, and *P. cephalalgicus* Clark & Galil 1993 could not be differentiated based on G1 morphologies, as the distinctions illustrated in Clark & Galil (1993: figs 2, 3, 11) appear to be attributable to size variation (see taxonomic account of *P. pilumnoides*). The G1 differences between *P. philippinesis* and *P. granulatus* outlined by Davie (2005) also appears to be due to variation—i.e., the differences in the distal lobes displays gradual variation. Specimens of *S. flava* comprise two distinct G1 morphologies. Specimens of *Chlorodiella davaoensis*, *Chl. cytherea*, and *Chl. crispipleopa* could not be separated based on G1 morphology. Differences outlined by Dai, Yang, Song, & Chen (1986) appeared to be intraspecific variation (see taxonomic account of *Chl. cytherea*). Specimens examined of *P. drachi* (not included in molecular analysis) and *P. granulatus* could not be differentiated based on G1 morphology. Specimens of *C. nigra* had a G1 morphology that was distinct from other species but with slight variation in size of distal lobe (Pl. 39B, C).

Specimens of *Chl spinimera* seemed to have a juvenile form of the *Chl. nigra* G1 morphology (see taxonomic account of *Chl. nigra*).

<u>Molecular analyses</u>

COXI gene tree models selected by JModeltest version 2.1.4 for *Chlorodiella*, *Cyclodius*, *Luniella*, *Pilodius*, and *Soliella* were TrN+G, TrN+I, HKY+G, HKY+G, and HKY+G, respectively. The average standard deviation

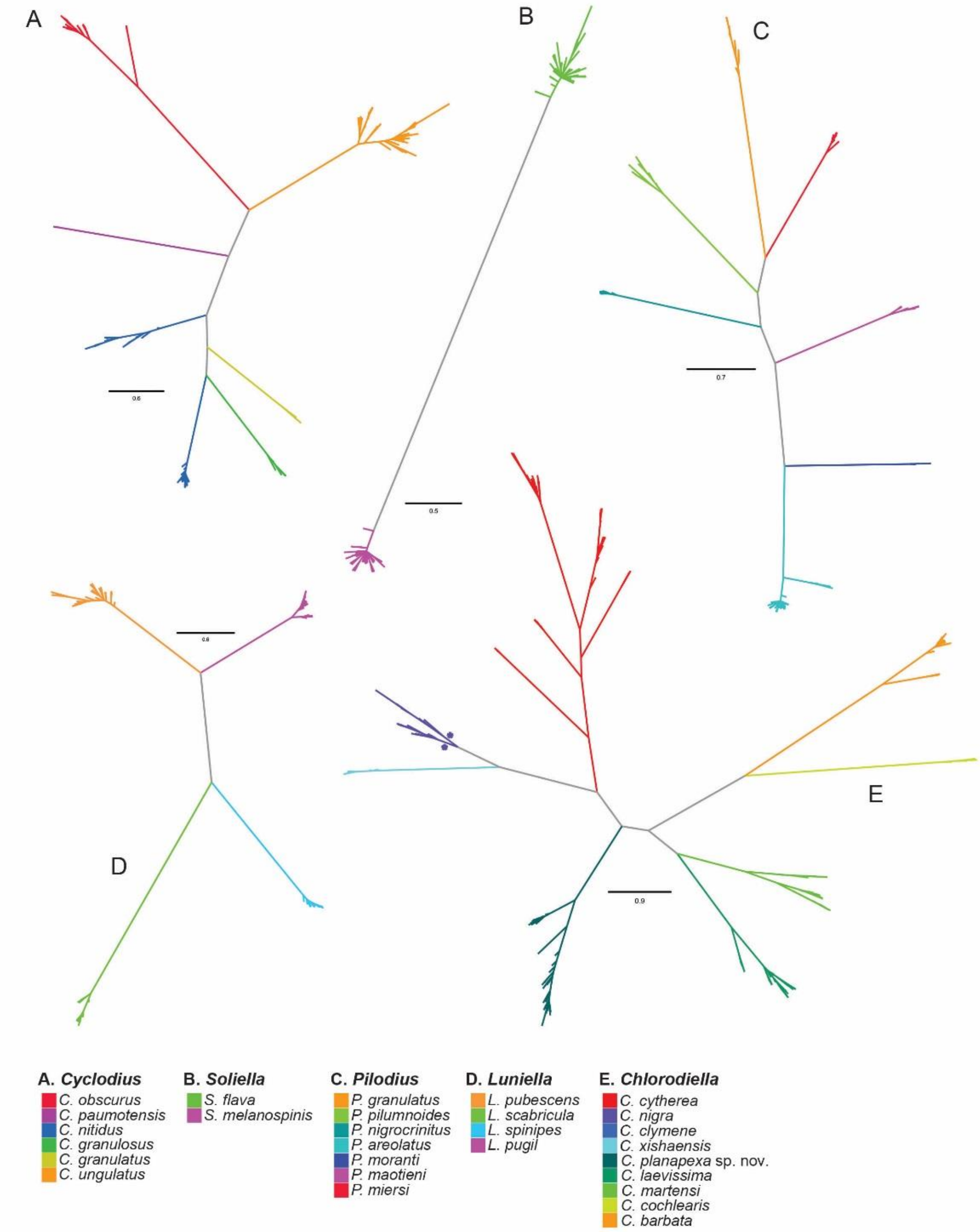

Figure 14. Bayesian Inference COXI gene trees for chlorodielline genera: A) *Cyclodius*; B) *Soliella*; C) *Pilodius*; D) *Luniella*; and E) *Chlorodiella*.

of split frequencies in the Bayesian analyses reached 0.010813, 0.008036, 0.004015, 0.005963, and 0.004971 after 10 million generations in the *Chlorodiella*, *Cyclodius*, *Luniella*, *Pilodius*, and *Soliella* analyses, respectively. Convergence of the two runs in all analyses was confirmed using Tracer version 1.5 (Rambaut & Drummond 2009). Clade support was assessed with posterior probabilities (pP) and 1000 bootstrap (BS) replicates in the BI and ML analyses, respectively.

The genetrees of *Chlorodiella*, *Cyclodius*, *Luniella*, *Pilodius*, and *Soliella* recovered 15, 8, 4, 7 and 2 reciprocally monophyletic, well supported (BS ≥ 70 and pP ≥ 0.95) clades. Most currently recognized species (Ng *et al*. 2008) were monophyletic and well supported. However, there were several notable exceptions. *Chlorodiella nigra* and *Chl. xishaensis* were recovered together in a monophyletic clade. Within this clade, the monophyly of *Chl. xishaensis* was supported. However, *Chl. nigra* was recovered as a monophyletic lineage but with low support. Specimens identified as *P. pilumnoides*, *P. concors*, and *P. cephalalgicus* were polyphyletic but recovered together in a well-supported, monophyletic clade [*P. pilumnoides* (*s. lat*.)]. Furthermore, several species were monophyletic and well supported, but recovered with well-supported, reciprocally monophyletic subclades: 1) *Chl. laevissima* (6 clades); 2) *Chl. barbata* (2 clades); 3) *Chl. nitidus* (2 clades); and 4) *Chl obscurus* (2 clades) (Fig. 14). Lastly, specimens of *Chl.*

Table 1. List of species in COXI gene trees with distance values with posterior probabilities (pP) and bootstrap values (BS) from BI and ML analyses, respectively. N = number of sequences included in analyses. "=" means cluster is equivalent to clade.

Taxon	Intraspecific variation	Smallest Interspecific Distance	pP	BS	N	# haplotypes	Species Identifier
Chlorodiella barbata	0–5.3	10.3	1	100	66	11	2 clusters
Chlorodiella barbata form 1	0–1.1	4.0	1	88	61	8	=
Chlorodiella barbata form 2	0–1.3	4.0	0.97	83	5	3	=
Chlorodiella coclearis	0–1.3	11.7	1	100	10	7	=
Chlorodiella cytherea	0–12.2	9.3	1	98	96	52	5 clusters
Chlorodiella cytherea form 1	0–2.9	7.7	1	100	39	28	=
Chlorodiella cytherea form 2	0	6.1	1	100	14	1	=
Chlorodiella cytherea form 3	1.6–1.9	6.9	1	100	3	3	=
Chlorodiella cytherea form 4	0–2.7	6.1	1	95	35	15	=
Chlorodiella cytherea form 5	0–0.5	9.0	1	100	5	5	=
Chlorodiella laevissima	0–4.5	6.6	1	97	61	20	2 clusters
*Chlorodiella martensi**	0–7.4	6.6	1	99	27	24	2 clusters
Chlorodiella martensi form 1	0–1.9	4.8	1	98	11	10	n/a
Chlorodiella martensi form 2	0–1.1	3.2	1	98	7	4	n/a
Chlorodiella martensi form 3	0–1.3	3.2	1	88	19	10	=
Chlorodiella planapexa sp. nov.	0–4.5	7.7	1	97	113	48	=
Chlorodiella planapexa form 1	0–0.8	2.9	1	82	38	18	n/a
Chlorodiella planapexa form 2	0–4.0	2.9	0.95	87	75	30	n/a
Chlorodiella nigra	0–4.8	6.6	0.88	99	41	25	=
Chlorodiella nigra form 1	0–3.2	2.1	0.86	n/a	13	12	n/a
Chlorodiella nigra form 2	0-1.6	2.1	0.79	40	28	13	n/a
Chlorodiella xishaensis	0–0.3	6.6	1	100	27	4	=
Cyclodius granulatus	0–1.4	7.6	1	100	3	2	=
Cyclodius granulosus	0–0.1	5.8	1	100	9	7	=
Cyclodius nitidus	0–9.1	5.8	n/a	n/a	52	20	2 clusters
Cyclodius nitidus form 1	0–0.4	5.8	1	100	34	6	=
Cyclodius nitidus form 2	0–2.8	5.8	1	78	18	14	=
Cyclodius obscurus	0–5.8	11.5	1	100	31	14	2 clusters
Cyclodius obscurus form 1	0–0.8	5.4	1	76	28	13	=
Cyclodius obscurus form 2	0	5.4	1	100	3	1	=
Cyclodius paumotensis	0	10.1	1	100	3	1	=
Cyclodius ungulatus	0–3.2	10.7	1	100	55	37	=
Luniella scabriculus	0–1.2	12.8	1	100	16	6	=
Luniella spinipes	0–0.2	11.4	1	92	15	4	=
Luniella pubescens	0–0.6	8.3	1	75	29	20	=
Luniella pugil	0–0.8	8.3	1	91	22	8	=
Pilodius nigrocrinitus	0–0.4	11.4	1	100	11	3	=
Pilodius pilumnoides	0–2.9	10.2	1	100	14	9	=
Pilodius maotieni	0–1.2	10.2	1	100	12	5	=
Pilodius miersi	0–0.8	10.6	1	100	14	3	=
Pilodius granulatus	0–2.3	11.2	1	100	12	8	=
Pilodius moranti	0–0.8	9.4	1	100	4	4	=
Pilodius areolatus	0–2.7	9.4	1	99	57	8	=
Soliella flava	0–1.4	12.0	1	100	45	6	=
Soliella melanospinis	0–0.8	12.0	1	100	39	16	=

recovered together in a well-supported clade. This clade comprised 5 reciprocally monophyletic, well supported subclades, but the divisions did not follow carapace and G1 morphological differences from literature (Fig 14).

For the concatenated dataset, models selected by JModeltest version 2.1.4 for COXI, 12S and 16S rRNA genes, and Histone H3 were TIM3+I+G, HKY+I+G, TrN+I+G, and HKY+I+G, respectively. The average standard deviation of split frequencies reached 0.002986 after 10 million generations. BI, ML and MP analyses recovered congruent topologies except where

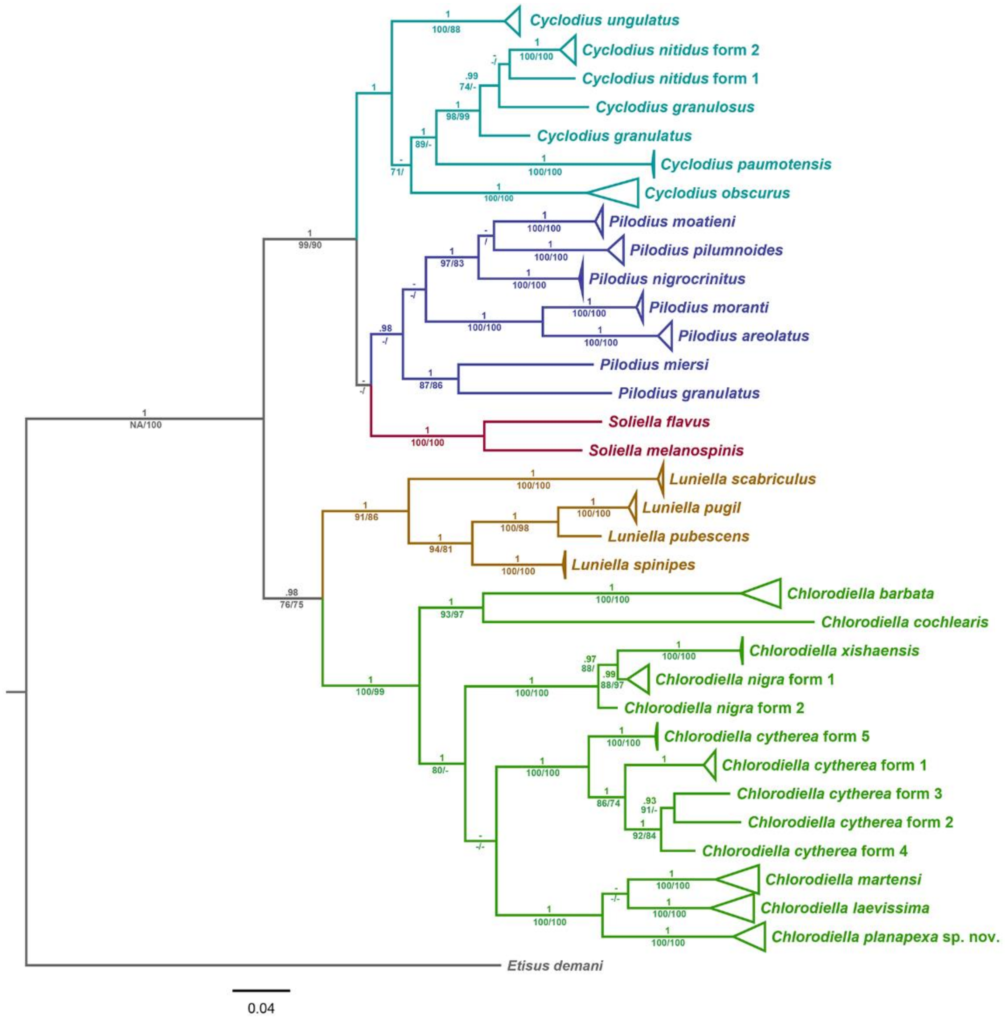

Figure 15. Bayesian consensus tree inferred from combined 12S, 16S, COXI, and H3 sequences. Numbers above, below left, and below right indicate Bayesian Inference posterior probability (pP), maximum likelihood bootstrap support (ML BS), and maximum parsimony bootstrap (MP BS) support, respectively. The latter two support values are separated by "/". Values below 95 (pP) and 70 (ML BS and MP BS) are represented by "–". Missing bootstrap values indicate clades not recovered in ML or MP analyses.

support values were low. The topology was similar to the chlorodielline clade recovered in the xanthid phylogeny (Chapter 3), but with greater taxon coverage, and reiterated intrafamilial relationships (Fig. 15, see General Discussion and Conclusion). The *Chlorodiella*, *Cyclodius*, *Luniella*, and *Soliella* clades were recovered with high support values in each analysis (BI, ML, and MP). The *Pilodius* clade was recovered in all analyses but with low support values in the ML and MP analyses. The clade was well supported in the BI analysis. The same species clades as in the COXI genetree analyses were recovered with one exception. *Chlorodiella nigra* was polyphyletic. One *Chl. nigra* clade was sister to *Chl. xishaensis* while the other was basal to these clades. The larger clade containing the three *Chl. nigra*-*Chl. xishaensis* clades was well supported. However, the *Chl. nigra*-*Chl. xishaensis* sister clade was not recovered in the MP analysis despite high support in the BI and ML analyses.

In the (3% threshold) SpeiciesIdentifier analysis, all reciprocally monophyletic clades of *Pilodius, Cyclodius*, *Soliella*, and *Luniella* from the COXI genetree analysis were recovered as equivalent “clusters”. However, only five clusters were found in the analysis of *Chlorodiella laevissima*, and these did not correspond with the six reciprocally monophyletic clades in the COXI genetree analyses. Although, each of the reciprocally monophyletic clades were recovered as clusters when the threshold was changed (see discussion below). Additionally, each of the reciprocally monophyletic clades from the COXI genetree analyses had a barcoding gap, with the exception of one of the *Chl. laevissima* subclades (see discussion below).

Combined Data

Of the 30 species with morphological and molecular data available that were included in the study, 27 distinct G1 morphologies were found. In the COXI genetree analysis, 36 reciprocally monophyletic, well-supported clades were recovered. All of these clades had a substantial barcoding gap except one of the *Chl. laevissima* clades (see below). The cluster analysis generated 36 clusters, but these clusters were not equivalent to the 36 COXI genetree clades. These results indicate clear conflict between currently recognized taxa, and delineation based on G1 morphology or sequence data.

Discussion

The evident conflicts between data fall into several categories. Several species could not be differentiated based on G1 morphology alone. This may indicate that G1 morphology is not a good indicator of species boundaries. Alternatively, it may indicate poor taxonomy. Conflict between morphological and COXI data may be due to incomplete lineage sorting, differences between evolutionary rates of COXI and isolating mechanisms, or insufficient sampling. Each species where conflict has arisen is discussed with these considerations in mind.

Incongruence between current taxonomy and G1 morphology

There were a few cases where G1, monophyly, barcoding gap, and cluster analysis at a 3% threshold were congruent but in conflict with the currently accepted species. Two such examples were: 1) *P. pilumnoides*, *P. concors*, and *P. cephalalgicus*; and 2) *P. granulatus* and *P. philippinensis*. In both cases, examination of the G1 morphology of numerous specimens indicated that the differences illustrated in literature between species, most importantly G1 morphology, was due to variation (Clark & Galil 1993, Davie 2005) (see taxonomic accounts). These observations were confirmed with molecular analyses. Each of the morphospecies, based on G1 morphology, were recovered within one monophyletic clade each in the COXI and combined analyses. Furthermore, the two clades had substantial barcoding gaps and were recovered as individual clusters in the cluster analysis (Table 1). Each of these clades are regarded as single species. Synonymy is discussed in taxonomic accounts below.

Another example of incongruence between G1 morphology and current taxonomy was within *S. flava*. After morphological examination of numerous specimens, two distinct G1 morphologies were uncovered (Pls 44, 45). These morphological differences were supported by reciprocal monophyly in the COXI and combined analyses, and by substantial barcode gaps and clusters equivalent to monophyletic clades. In fact, the distance between these two clades was the second highest between sibling species in the subfamily (smallest interspecific distance = 12%). These data indicate that *S. flava* comprises two species: *S. flava* and the junior synonym, *S. melanospinis* (see taxonomic accounts).

There were a couple of more complicated incompatibilities between G1 morphology and current taxonomy. *Chlorodiella cytherea*, *Chl.*

davaoensis, and *Chl. cytherea* all have a similar hooked or curled G1 tip. In their description of *Chl. crispipleopa*, Dai *et al*. (1986) stated that the species differs from *Chl. cytherea* in having a “curled” tip (versus “hooked” in *Chl. cytherea*). The authors also outlined several other external differences between the two species. *Chlorodiella davaoensis* was not mentioned in their treatment. However, an examination of the holotype revealed that the G1 is of the hooked type. After examination of hundreds of specimens, it became clear that the hooked form grades into the curled form—i.e., there are intermediates. This character could not be reliably used for delineation among the three species and neither could the external characters outlined by Dai *et al*., as they were also variable (see taxonomic account). Based on these data, the three species are conspecific. The specimens examined were recovered in a well-supported monophyletic clade in the COXI and combined analyses. However, the intraspecific variation of the clade was very high, (0–12.2), there was no barcoding gap between this clade and its closest sibling species, and there were five reciprocally monophyletic, well-supported subclades within this larger clade. Each of these subclades was supported by a substantial barcoding gap and each was recovered as a separate cluster (Table 1). Three of these clades contained both hooked and curled G1s, one comprised only three female or juvenile specimens, and the remaining clade contained specimens with only the curled morphology. G1 morphology was not useful for delineating the subclades of the *Chl. cytherea*. However, G1 morphology did support the larger *Chl. cytherea* monophyletic group and indicated that the currently defined boundaries are in need of further examination (see taxonomic account).

The *Chl. laevissima* complex was another complicated example. Despite congruence of external morphology of all *Chl. laevissima* specimens examined, three distinct G1 morphologies were uncovered. The structures of these three different G1 morphologies are very similar to one another, especially when compared with other species of *Chlorodiella,* yet they are distinct, without intermediates. Furthermore, each morphology was recovered in a well-supported monophyletic clade. The species status is discussed below. However, the clades are henceforth referred to as *Chl. laevissima, Chl. martensi* and *Chl. planapexa* sp. nov. for clarity (see taxonomic accounts) (Figs 14, 15).

The presence of subclades within morphological species was another complication. The *Chl. martensi* and *Chl. planapexa* clades were divided into three and two subclades, respectively. Each of these subclades were reciprocally monophyletic and well-supported in the COXI and combined analyses. All of the subclades had a small barcoding gap except one of the *Chl. planapexa* clades (form 2, see below) (Table 1, Fig. 14). However, the cluster analysis conflicted with the clades supported by the COXI and combined analyses. Two clusters were detected for the one *Chl. laevissima* clade recovered in the COXI genetree; only two clusters were detected for *Chl. martensi*, despite its three subclades in the COXI genetree; and only one cluster was detected for the two subclades of *Chl. planapexa* in the COXI genetree. In summary, G1 morphology was useful in delimiting three monophyletic clades within the current taxon *Chl. laevissima* but not for delineating subclades. The molecular analyses also were not in congruence with respect to the subclades.

Incongruence between G1 morphology and monophyly

The two cases of incongruence between G1 morphology and monophyly are noteworthy. All *Cyclodius nitidus* specimens examined in this study have the same G1 morphology, with slight variation in number of setae.

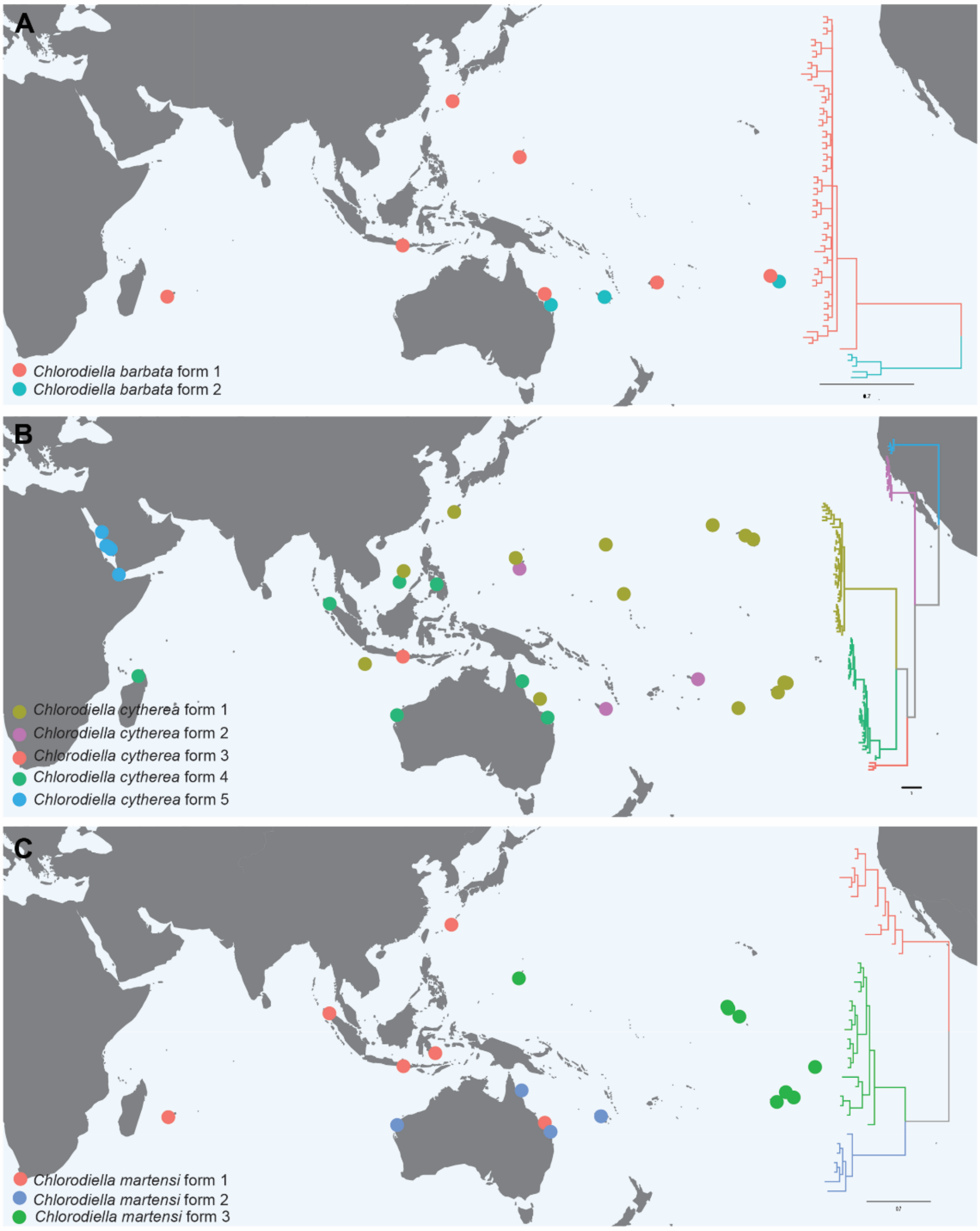

Figure 16. Geographic variants of: A) *Chlorodiella barbata*; B) *Chl. cytherea*; and C) *Chl. martensi*.

However, two well-supported clades were recovered for these specimens. Each clade is further delineated by a congruent cluster and substantial barcoding gap. However, the COXI genetree analyses recovered one *Cyclodius nitidus* clade in a basal position to a large clade comprising the other *Cyc. nitidus* clade, *Cyc. granulosus*, and *Cyc. granulatus*—i.e., the two *Cyc. nitidus* clades were not recovered as sibling species. These relationships were well supported in the ML analysis and generally so in the

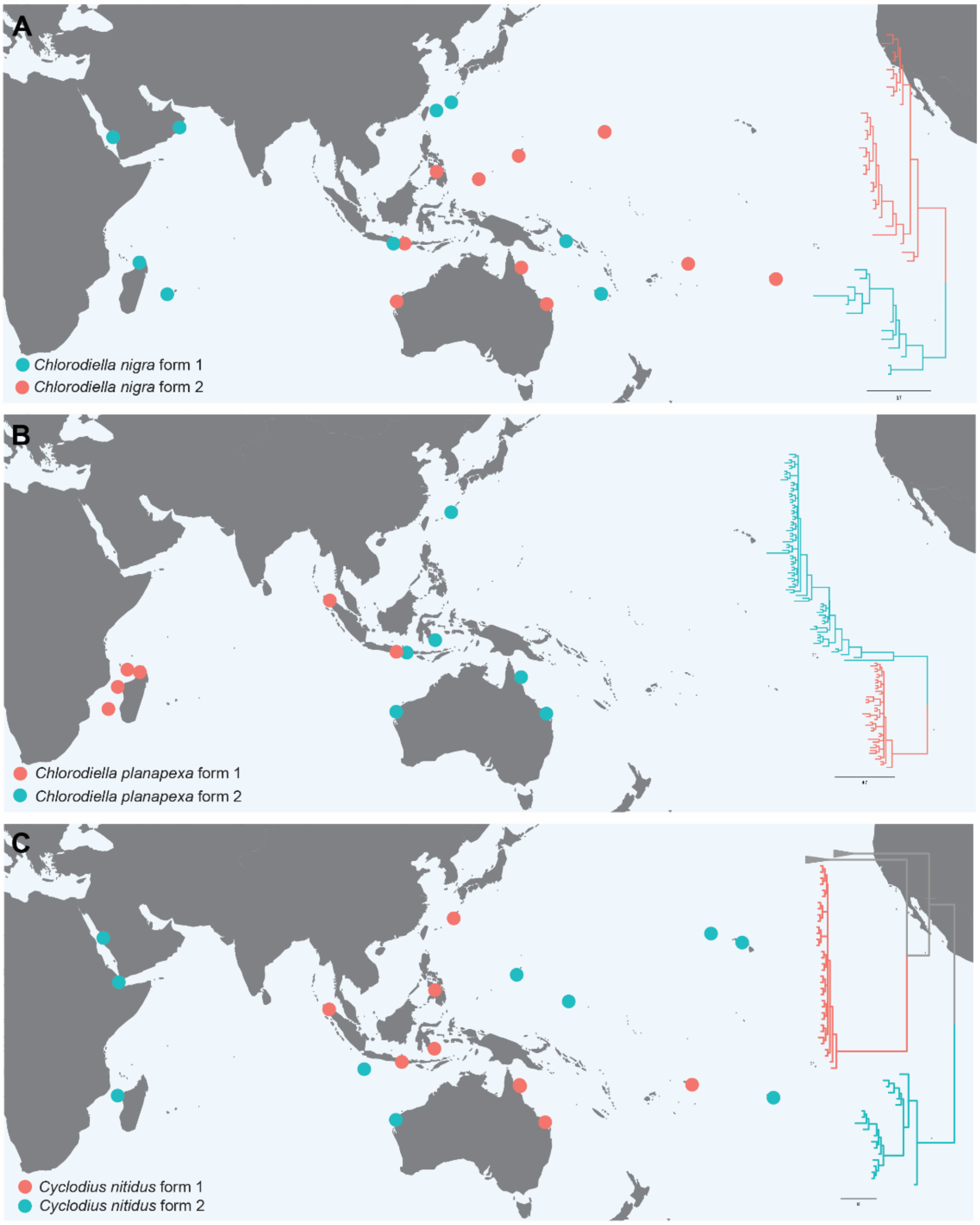

Figure 17. Geographic variants of: A) *Chlorodiella nigra*; B) *Chl. planapexa*; and C) *Cyclodius nitidus*.

BI analysis. However, in the combined analysis (12S, 16S, COXI, and H3), the two were sibling clades in the ML and BI analyses, although with low support. The sibling clade relationship was not recovered in the MP analysis. It is unclear whether these clades represent sibling subclades within a larger *Cyc. nitidus* clade, or if they are polyphyletic lineages with undifferentiated G1s. Until more data are available and for further discussion, the clades are

Figure 18. Geographic variants of *Cyclodius obscurus*

referred to as “forms” of *Cyc. nitidus*—i.e., *Cyc. nitidus* form 1 and *Cyc. nitidus* form 2 (see taxonomic account).

The other example of incongruence between G1 morphology and monophyly involves *Chl. nigra*, *Chl. spinipes,* and *Chl. xishaensis*. The G1 morphology of *Chl. nigra* and *Chl. spinipes* are indistinguishable. The description of *Chl. spinipes* is clearly based on a juvenile *Chl. nigra* specimen and is therefore regarded as a junior synonym (see taxonomic account). The COXI genetree analyses did not recover *Chl. nigra* with high support. Furthermore, *Chl. nigra* was polyphyletic in the combined analyses. One *Chl. nigra* clade was recovered in a basal position with respect to the other *Chl. nigra* clade and *Chl. xishaensis*. This sibling species relationship between one of the *Chl. nigra* clades and *Chl. xishaensis* was well supported in the ML and BI analyses but not recovered in the MP analysis. *Chl. xishaensis*, on the other hand, has a very distinct G1 morphology and was recovered with high support in the COXI genetree and concatenated dataset analyses. It was also supported by a substantial barcoding gap and cluster. The two *Chl. nigra* clades are referred to as forms—i.e., *Chl. nigra* form 1 and *Chl. nigra* form 2 (see taxonomic accounts). The smallest interspecific distance in the COXI between the *Chl. nigra* clades is only 2.1%, compared with intraspecific variation of 0–1.6 and 0–3.2. The distance between these clades is lower than any of the reciprocally monophyletic, well-supported clades recovered, and again, the clades were not well-supported in the COXI analyses.

The fact that the *Chl. nigra* form 1 and *Chl. nigra* form 2 clades are paraphyletic in the combined analysis raises questions. *Chlorodiella nigra* form 1 has slight variation in G1 morphology, although many specimens have G1s that are indistinguishable from the *Chl. nigra* form 2 morphology (see taxonomic account). These may be incipient species, or if monophyly were used as criterion for delineation, full species. However, it is also possible that the species is simply paraphyletic, with *Chl. xishaensis* having stemmed from a peripheral population. This would not be surprising, as an estimated 20% of species are paraphyletic (Funk & Omland 2003; Ross 2014).

Geographic variants as subclades

G1 morphology was in concordance with current taxonomy for the remaining species. However, there were several well-supported, monophyletic clades dividing several of the G1 morphospecies into subclades. A few G1 morphospecies and their subclades were previously mentioned (number of subclades indicated): *Chl. cytherea* (5), *Chl. planapexa* sp. nov. (2), *Chl. martensi* (3), *Cyc. nitidus* (2), and *Chl. nigra* (2). Additionally, *Chl. barbata* and *Cyc. obscurus* were monophyletic in the COXI genetree and combined analyses, but with two well-supported, reciprocally monophyletic subclades each (Fig. 14). These clades are supported with substantial barcoding gaps and clusters congruent with their respective clades.

Each of these subclades has a distinct geographic signal with respect to other subclades sharing the same G1 morphology. For example, the five subclades in the monophyletic *Chl. cytherea* morphotype are allopatric, parapatric, or relatively narrowly distributed at the periphery of the other species ranges (peripatric). *Chlorodiella nigra* has two subclades that have Indian Ocean versus Pacific Ocean distributions, with overlap in the Coral Triangle region. *Chlorodiella martensi* comprises clades with three distinct distributions: 1) Indian Ocean and the coral triangle area; 2) northern Australia to New Caledonia; and 3) Pacific oceania. *Chlorodiella planapexa* comprises two subclades with two distinct distributions: 1) Indian Ocean to southern coral triangle; and 2) Coral Triangle and adjacent areas. The subclades of *Chl. barbata* were interesting as one had a widespread IWP distribution while the other was restricted to a long belt along the southern Western Pacific. *Cyclodius nitidus* comprised two clades, one with a disjunct IWP distribution and the other restricted to the Coral Triangle and adjacent areas. Last, *Cyc. obscurus* was composed of a clade with a widespread IWP distribution and one restricted to the Hawaiian Islands.

These subclades may represent incipient species, in which gonopodal and other morphological differences have not yet evolved. There are a few examples of variation within one or more sister subclades that may indicate morphological differentiation. Three of five *Chl. nigra* subclades have variable G1s. The same is true of *Chl. nigra* form 1. Furthermore, the external morphology of *Cyc. nitidus* form 2 is variable (see taxonomic account of *Cyc. nitidus*). Whether or not these clades represent incipient species, subspecies, or even new species remains to be tested. Further work including more nuclear markers and morphometric studies may shed light on these subclades.

Systematic Account

Subfamily Chlorodiellinae Ng & Holthuis, 2007

Chlorodinae Alcock 1898: 78, 156 (part). — Sakai 1976: 385, 454 (in part).

Chlorodiinae, Serène 1968: 80 (part). — Takeda 1976: 70.

Chlorodioida, Alcock 1898: 78, 159 (part). — Sakai 1976: 385, 455 (part).

Chlorodiellinae Ng & Holthuis 2007: 19.

Key to the Genera of Chlorodiellinae Ng & Holthuis, 2007.

1. Dorsal surface of carapace appearing smooth without magnification. Regions poorly or not defined..*Chlorodiella*
– Dorsal surface of carapace with smooth, granulate or setose regions. Regions well defined...2
2. Anterolateral angle of basal antennal segment expanded forming flange, entering halfway into or completely filling orbital hiatus (Fig. 10C, E)...3
– Anterolateral angle of basal antennal segment not or slightly expanded, entering less than halfway into orbital hiatus (Fig. 10A, B, D, F)...4
3. Apical lobe of G1 flat and arched or twisted (Pl. 42).................*Luniella*
– Apical lobe of G1 spatulate, hooked or recurved, never flatten and arched or twisted...*Pilodius*
4. Dorsal surface of carapace without setae [or setose and having G1 with ovoid apical opening in *Cyc. paumotensis* (Pl. 41B)].......*Cyclodius*

– Dorsal surface of carapace covered with short and long light-colored setae. G1 apex spatulate and almost tubular or longitudinally hollowed (Pls 44D, 45)..*Soliella*

Chlorodiella Rathbun, 1897

Chlorodius H. Milne Edwards 1834: 399. — De Haan 1835: 13. — Dana 1851: 123; 1852: 204. — A. Milne-Edwards 1873: 212. — Alcock 1898: 159. — Borradaile 1902: 259. — Odhner 1925: 85.

Chlorodiella Rathbun 1897: 57; 1930: 462. — Balss, 1922b: 130; 1938a: 51 — Gordon 1934: 49. — Ward: 1939: 10; 1941: 10; 1942b: 97. — Sakai 1939: 508; 1965; 1976: 464. — Barnard 1950: 213. — Forest & Guinot 1961: 95. — Miyake & Takeda 1968: 391. — Chen & Lan 1978: 267. — Miyake 1983.

Key to the Species of *Chlorodiella*.

1. Anterolateral margin of carapace with 3 low, rounded lobular teeth excluding outer supraorbital lobular tooth....................*Chl. quadrilobata*

– Anterolateral margin of carapace with 2 to 4 anterolateral teeth excluding outer supraorbital tooth, at least one of which is spinose, triangular or otherwise pointed...2

2. Anterolateral margin of carapace with 2 or 3 teeth excluding outer supraorbital tooth...3

– Anterolateral margin of carapace with 4 teeth excluding outer supraorbital tooth...5

3. Anterolateral margin of carapace with long lobe followed by 1 large anteriorly directed, sharp tooth, and 1 laterally directed, minute tooth..*Chl. ohshimai*

– Anterolateral margin of carapace with 3 teeth excluding outer supraorbital tooth...4

4. Chelae with tuft of numerous setae on articulation of fingers...*Chl. barbata*

– Chelae without tuft of setae at articulation of fingers......*Chl. cochlearis*

5. Pterygostomial region without setae. G1 with numerous relatively long subdistal setae and spatulate apex (*Chl. laevissima* complex)............6

– Pterygostomial region with plumose setae diagonally from posterior to lateral surface. G1 with apex curled, hooked, or spatulate. If spatulate, with relatively short setae...7

6. Apical lobe of G1 flattened, triangular (Pl. 38C)..*Chl. planapexa* sp. nov.

– Apical lobe of G1 truncate, spatulate, distal margin rounded (Pl. 38D)...*Chl. laevissima*

– Apical lobe of G1 long, spatulate, convex in cross section, tip pointed (Pl. 39A)...*Chl. martensi*

7. Apex of G1 hooked or curled (Pls 37C, D, 38A, B). Lateral regions of carapace marked with low elevations or ridges................*Chl. cytherea*

– Apex of G1 spatulate, tip pointed. Lateral regions relatively more distinctly defined, elevations higher..8

8. Lateral regions of carapace granulate. Chelipeds relatively short. G1 relatively straight, apex spatulate with straight longitudinal margins (Pl. 39D)...*Chl. xishaensis*

– Lateral regions of carapace appearing smooth without magnification. Chelipeds relatively long. G1 curved 3/4 distance to tip, apex spatulate with convex anterior margin (Pl. 39B, C)................................*Chl. nigra*

Chlorodiella barbata (Borradaile, 1900)

Pls (1, 37A, 46A)

Chlorodius barbatus Borradaile 1900: 587, pl. 41, fig. 4 [Original description] [Funafuti, Rotuma]; 1902: 259, fig. 41D [Minikoi, Goifurfehendu and Miladumadulu Atolls (Maldive and Laccadive Archipelagos)]. — Bouvier 1915: 98 [Mauritius].

Chlorodius laevissimus, Grant & McCulloch 1906: 12 [Mast Head I., Australia]. (not *Chlorodiella laevissima* (Dana, 1852).

Chlorodiella barbata Rathbun 1911: 225 [Salomon lagoon and Egmont reef, Chagos]. — Balss 1934: 515 [Toliara, Toamasina, and Antsiranana, Madagascar; Reunion Island]; 1938a: 53 [Aranuka, Tabiteuea, and Abemama, Gilbert Islands; Jaluit Atoll, Marshall Islands; Viti Levu, Namuka, and Bau, Fiji]. — Ward 1932: 250 [North West Island, Australia]; 1939: 10 [Savaii Island, Samoa]; 1942: 97 [Salomon, Chagos Islands]. — Tweedie 1950b: 121 [Cocos (Keeling) Islands]. — Holthuis 1953: 14 [Saipan; Onotoa and Bikati Gilbert Islands]. — Barnard 1954: 98 [Europa Island]. — Forest & Guinot 1961: 96, figs. 93, 94, 99, 100 [Tahiti, Marutea Atoll, Mangareva]. — Michel 1964: 23 [Mauritius]. — Guinot 1967c: 262 [list]. — Serène 1968: 81 [List]; 1984: 260, fig. 170, pl. 36A [Nosy Be, Madagascar; Ile Europa; Iles Glorieuses; Reunion Island]. — Takeda & Nunomura 1976: 74 [Poum and Iloc Mouac (in the vicinity of Poum), New Caledonia]. — Peyrot-Clausade 1977a [Tulear, Madagascar]: 26; 1977b:

213 [Moorea]; 1989: 112 [Tikehau, Tuamotu]. — Chen & Lan 1978: 270, fig. 4, 7 (4-5), pl. 1, fig. 4 [Xisha Islands]. — Ribes 1978: 126 [Reunion I.]. — Thomassin, 1978: 3, 64 [Tulear, Madagascar]. — Dai *et* al. 1986: 314, fig. 168 (1), pl. 45 (3) [Review]. — Dai & Yang 1991: 339, fig. 168 (1), pl. 45 (3) [Review]. — Davie 2002: 518 [Review]. — Ng *et al*. 2008: 196 [List].

Material examined. *Reunion Island:* 1 male, 4.75 × 3.15 (UF 12567*), BREU-FM-0060-1, SWIO-FM30, 0-2 m, Saint-Gill Hermitage, La Réunion Island, Mascarene Islands, coll. N. Hubert & F. Michonneau, 22 July 2007. — 1 female, 6.70 × 4.60 (UF 12572*), BREU-FM-0096-1, SWIO-FM31, 0–2 m, -21.0941°, 55.2347°, Planch' Alizé, La Saline, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 23 July 2007. — 1 male, 7.25 × 4.85 (UF 17571), BREU-FM-0095-1, SWIO-FM31, 0–2 m, -21.0941°, 55.2347°, Planch' Alizé, La Saline, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 23 July 2007. — 1 female (UF 12589*), BREU-FM-0231-1, SWIO-FM35, 0–2 m, -21.1008°, 55.2437°, Trou d'eau, La Saline, La Réunion Island, Mascarene Islands, N. Hubert & F. Michonneau, 27 July 2007. — 1 male, 7.65 × 5.30 (UF 12644*), BREU-0217, SWIO-2, 0–1 m, -21.1072°, 55.2489°, on *Acropora*, fringing reef moat, Varangue du lagon, Saint-Paul, La Réunion, Mascarene Islands, coll. Bruggemann *et al*., 6 August 2007. — 1 female, 4.90 × 3.10 (UF 12647), BREU-0220, SWIO-2, 0–1 m, -21.1072°, 55.2489°, on *Acropora*, fringing reef moat, Varangue du lagon, Saint-Paul, La Réunion, Mascarene Islands, coll. H. Bruggemann *et al*., 6 August 2007. — 1 male, 7.50 × 4.90 (UF 12646*), BREU-0219, SWIO-2, 0–1 m, -21.1072°, 55.2489°, on *Acropora*, fringing reef moat, Varangue du lagon, Saint-Paul, La Réunion, Mascarene Islands, coll. H. Bruggemann *et al*., 6 August 2007. — 1 female, 7.50 × 4.80 (UF 12645*), BREU-0218, SWIO-2, 0–1 m, -21.1072°, 55.2489°, on *Acropora*, fringing reef moat, Varangue du lagon, Saint-Paul, La Réunion, Mascarene Islands, coll. H. Bruggemann *et al*., 6 August 2007.

Seychelles: 6 males, 3.4 × 2.3 – 6.1 × 4.0, 4 females, 3.2 × 2.2 – 3.2 × 2.2, 3 ovigerous females, 4.0 × 2.5 – 5.4 × 3.4, 2 juveniles (USNM 1188404), near Passe Dubois, lagoon, Aldabra Atoll, Seychelles, coll. B. Kensley, 21 March 1986.

Chagos: 2 males (larger = 3.4 × 2.2), 3 females, 5 juveniles (ZRC 2013.0772), CH0432, 10m approx., dead branching coral heads, lagoon, Peros Banhos Chagos Archipelago, coll. C. Head & H. Koldeway, 23 February 2013. — 2 males, 6.9 × 4.4 – 7.0 × 4.4, 3 females, 4.3 × 2.9 – 7.7 × 4.7 (USNM 41254), Egmont Reef, Chagos Archipelago, British Indian Ocean Territory, coll. J. Gardiner, Sealark Expedition, Sealark R/V, 1905.

Philippines: 1 male, 5.55 × 4.00 (ZRC 2010.0269), Stn. S34, 2 m, 9°38.3'N 123°50.3'E, mixed bottom, Sungcolan inlet, Panglao Island, Philippines, 9 June 2004. — 2 males, largest male = 6.70 × 4.60, 1 female (ZRC 2013.0373), Stn. B8, 3m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, 7 June 2004. — 1 male, 7.70 × 5.40 (ZRC 2013.0374), Stn. B34, 1-2 m, 9°38.3'N 123°50.3'E, channel between inlet and the open sea, Sungcolan inlet, Panglao Island, 28 Jun 2004. — 1 male, 4.4 × 2.9, 2 females, 4.4 × 2.9 – 5.8 × 3.5 (USNM 65273), 4 32 15 N 119 22 45 E, South of Centroid, Tumindao Reef, Sibutu Island, Sibutu Group, Sulu, Philippines, coll. United States Fish Commission, Philippines Expedition, Albatross R/V, 27 February 1908.

Indonesia: 1 male, 6.25 × 4.20 (ZRC rBALI-0081), hand collected, 0–10 cm, -8.71348°, 115.2516°, in rubble or seaweed, rocky substrate, hard exposed substrate with sandy patches, scattered coral, exposed (low tide), closest beach from Rama Villas, Sanur Beach, Bali, Indonesia, coll. R. Lasley *et al*., 15 June 2011. — 1 male (ZRC rBALI-0250), hand collected, snorkel, 1–3 m, rubble(?), sand, scattered coral, rubble, sea grass, under rocks or on *Porites*, Waha, right out front of office, Wangiwangi, Wakatobi, Sulawesi, Indonesia. — 3 males, largest male = 4.75 × 3.20, 4 ovigerous females, 1 juvenile (ZRC rBALI-0006), hand collected, 1 m, -8.71348°, 115.2516°, in seaweed, sea grass bed, point 400 meters east of beach outside of Rama Villa, Sanur Beach, Bali, Indonesia, coll. R. Lasley & V. Morgan, 15 June 2011. — 1 ovigerous female, 5.8 × 3.5 (ZRC 2013.1587), Stn. BL11-001, BALI-0005, 1 m, -8.71348° 115.2516°, hand collection, in sea weed, sea grass bed, point 400 meters east of beach nearest Rama Villa, Sanur Beach, Bali, Indonesia, coll. 15 June 2011.

Japan: 20 males, largest male = 9.30 × 6.65, 5 females, 6 ovigerous females (ZRC 1995.511), 4192, Sesoko Beach, Okinawa, Japan, coll. P. Ng. — 1 male, 6.2 × 4.2 (UF 27004*), Stn. GUOK10-St-071, 26.21218° 127.664291°, 1–8 m, silty harbor, river mouth, wharfs, Okinawa, Naha Harbor, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al*., 16 July 2010.

Palau: 2 males, 5.6 × 3.4 – 7.9 × 5.0, 1 female, 4.6 × 2.9 (USNM 1184806), 1 m, southeast, patch reef near Malakal Pass, Urukthapel Island, Palau, coll. R. Kropp, 20 June 1984. — 1 male, 4.1 × 2.5 (USNM 1184790), west of road by K-B bridge, Koror Island, Palau, coll. R. Kropp, 13 July 1984. — 1 female, 5.9 × 3.7 (USNM 1184762), 1 m, shallow fringing reef, west coast of island, Aulong Island, Palau, coll. J. Dominguez, 28 June 1984.

Caroline Islands: 1 male, 6.4 × 4.0 (USNM 134513), tidal flats, Balabat, Yap Island, Yap Islands, Caroline Islands, Micronesia, coll. R Hiat. — 1 female, 3.2 × 1.9 (USNM 255866), W tip of pass, Nanpinapu, Ant Atoll, Ponape, Caroline Islands, North Pacific Ocean, coll. Kropp, Birkeland, 17 November 1984.

Mariana Islands: 2 males, 5.1 × 3.2 – 5.9 × 4.1 (UF 2063*), ZZZ-086651, 10-20 ft, among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Islands, Mariana Islands, H. Conley, 12 March 2002. — 1 male, 6.90 × 4.65 (UF 2024*), ZZZ-086669, 3-6 ft, among dead coral and rocks, Orote Peninsula E of Neye Island, Guam, Mariana Islands, coll. H. Conley & F. Schroeder, 7 April 2002. — 1 female, 5.30 × 3.40 (UF 2902*), ZZZ-087499, 1-3 ft, among coral rubble and rocks, NE side Alutom Islet, Guam Island, Mariana Islands, coll. H. Conley, 6 June 2002. — 1 male, 6.75 × 4.35 (UF 2729), ZZZ-087507, 10-20 ft, among rocks, near harbor, Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, USA, coll. H. Conley, 13 June 2002. — 4 males, largest male = 7.50 × 4.80, 5 ovigerous females (UF 2962*), ZZZ-087514, 4-8 ft, among rocks, approximately midway along Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 18 June 2002. — 1 ovigerous female, 6.40 × 4.05 (UF 2881*), ZZZ-087517, 2-10 ft, among and under dead coral and rocks, Western Shoals, Apra Harbor, Guam Island, Mariana Island, coll. H. Conley, 21 June 2002. — 2 males, 4.5 × 2.9 – 5.0 × 3.1 (USNM 94055), Lagoon west of Saipan, Saipan Island, Northern Mariana Islands, coll. P. Cloud, 3 May 1949.

Great Barrier Reef: 1 female, 8.45 ×5.30 (UF 17105*), AUST-1154, AUST-ST-049, 1-2 m, -14.7429°, 145.5143°, dip net, hand, under rocks and in rubble, reef flat, North Direction Island, S of Lizard Island, Queensland, Australia, coll. A. Anker & R. Lasley, 17 February 2009. — 1 male (UF 25244*), AUST-5548, HI09-042, Heron Island, Queensland, Australia, coll. 17 November 2009. — 1 male (25612*), AUST-6063, HI09-090, 4–10 m, algae covered dead *Pocillopora damicornis*, outer reef, exposed, Heron Island, Queensland, Australia, coll. J. Reimer & F. Michonneau, 23 November 2009. — 1 male, 8.3 × 5.2 (UF 25049*), AUST-5255, HI09-037, -23.4418°

151.9004°, in rubble, Heron Island, Queensland, Australia, coll. 16 November 2009.

New Caledonia: 2 males, 6.7 × 4.2 – 6.7 × 4.5 (UF 37981*), NewC13-184, NEST9, 1–2 m, -22.6681° 167.425°, coral breaking, coral rubble, coralline algae, Ile des Pins, New Caledonia, coll. N. Evans, 2 November 2013.

Vanuatu: 7 males, 3.8 × 2.5 – 5.2 × 3.2, 2 females, 3.7 × 2.3 – 4.5 × 2.9, 3 ovigerous females, 4.0 × 2.6 – 6.0 × 3.1, 3 juveniles (ZRC 2013.1588), Stn. FB52, 7m, 15°42.7'S, 167°15.1'E, dead coral patches with algae, Malokilikili, Vanuatu, coll. Santo Marine Biodiversity Survey, 05 October 2006. — 5 males, 3.2 × 2.0 – 6.8 × 4.3, 5 females, 5.8 × 3.1 – 4.0 × 2.1 (ZRC 2013.1589), Stn. ZB36, intertidal, 15°34.3'S, 167°12.4'E, under rocks, E Aoré island, Aisari Bay, Vanuatu, coll. Santo Marine Biodiversity Survey, 19 October 2006.

Marshall Islands: 10 males, largest male = 7.05 × 4.65, 6 females, 1 juvenile (UF 13412), FM-MAJ-047, FM-St-MAJ08-02, 0-2 m, 7.1652°, 171.0361°, cryptofauna, rubble, corals, seagrass bed, sand, reef flat, N end of the island, ocean side, Laura, Marshall Island, Republic of the Marshall Islands, coll. F. Michonneau & S. Kim, 4 April 2008. — 1 male, 5.3 × 3.4 (USNM 1181222), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt, 1950.

Kiribati: 1 male, 5.9 × 3.7, 1 female, 5.7 × 3.6 (USNM 33261), reef, shore, Gilbert Islands, Kiribati, coll. Albatross, 6 January 1900. — 1 male, 8.2 × 5.1 (USNM 1181249), Kanton Island, Kiribati, coll. L. Schultz, 1939.

Fiji: 1 male, 6.35 × 4.20, 1 female, 1 juv. (UF 1740*), LAK-005L, 0-1 m, under rock, 125 feet from shore, behind Usp Maritime Studies Buildings, Laucala Bay, Viti Levu Island, Fiji, coll. L. Kirkendale & V. Bonito, 6 October 2001.

Tuvalu: 8 males, 4.0 × 3.1 – 6.2 × 4.1, 9 females, 3.8 × 2.5 – 5.7 × 3.7 (USNM 33258), Ellice Island, Funafuti Atoll, Tuvalu, coll. Albatross R/V, 24 December 1899.

Samoa: 2 males, largest male = 5.68 x 3.70 (AMNH 7580), Western Samoa, 18 October 1936. — 1 male, 5.0 × 3.2 (USNM 1181256), Pago Pago, Tutuila Island, American Samoa. — 1 male, 6.5 × 4.2 (USNM 1181220), coral reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, July 1902.

Gambier Islands: 1 female, 4.9 × 3.2 (UF 35501), 0.5 m, -23.1517° -135.0554° in small bay, Terevai Island, Gambier Islands, French Polynesia, coll. J. Moore & C. Payri, 8 February 2013.

Society Islands: 1 male (UF 10094*), BMOO-324, GP Loc-858, 0-2 m, -17.4875°, -149.8264°, fringing reef flat in bay(?), NW side of Cook's Bay, Moorea Island, coll. G. Paulay, 12-19 June 2006. — 3 males, largest male = 5.25 × 3.55, 9 females (UF 9854*), BMOO-1187, GP-Loc-878, 0-2 m, -17.4982°, -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 male, 5.20 × 3.65 (UF 9856*), BMOO-1185, GP-Loc-878, 0-2 m, -17.4982°, -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 male, 4.65 × 3.10 (UF 9855*), BMOO-1186, GP-Loc-878, 0-2 m, -17.4982°, -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 male, 8.1 × 5.10 (UF 16449), BMOO_5494, MIB_212, 0-2 m, under coral rocks, from crevices in dead coral, silt-covered fringing reef, Gump-CRIOBE road, 200 m before Sheraton, Moorea, Society Islands, French Polynesia, coll. A. Anker, 16 November 2008. — 7 males, 3.7 × 2.2 – 7.4 × 4.7, 5 females, 3.3 × 2.1 – 6.4 × 3.9 (USNM 1181257), reef NW of Moty Uta Island, Papeete Harbor, Tahiti, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 19 April 1957. — 4 males, 3.3 × 2.2 – 6.3 × 4.1, 2 females, 3.3 × 2.1 – 3.8 × 2.6 (USNM 1181229), head of Baie de Maroe, Maroe Bay, Huahine, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 30 April 1957. — 3 males, 4.3 × 2.8 – 6.2 × 3.9, 1 female, 5.2 × 3.3 (USNM 1181236), algae, half mile south of Farepiti Point, Bora Bora, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 23 April 1957. — 4 males, 4.4 × 2.9 – 5.8 × 3.6 (USNM 1181246), Tetaro Island, Raiatea, Society Islands, French Polynesia.

Tuamotu Islands: 1 male, 7.6 × 4.8 (USNM 1181253), Lagoon Cove, Maiai Island, Tikehau Atoll, Tuamotu Archipelago, French Polynesia, coll. Bredin Pacific Expedition, 13 April 1957. — 1 male, 5.1 × 3.3 (UF 35301), Stn. HAO-003, -18.06897° -140.984929°, 0.5–3 m, fringing reef and back reef, Hao Atoll, near red channel marker, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 18 January 2013. — 1 male, 7.1 × 4.5 (UF 35306), Stn. HAO-003, -18.06897° -140.984929°, 0.5–3 m, fringing reef and back reef, Hao Atoll, near red channel marker, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 18 January 2013.

Diagnosis. Carapace (Pl. 1A, B) transversely hexagonal, relatively broad, ca. 1.5–1.6 broad as long; surface smooth, laterally minutely granulate, regions poorly or undefined with H-shape groove at posterior border of 3M. Front (Pl. 1C) broad, deflexed, submedian lobes weakly convex, separated by shallow V-shaped notch. Anterolateral margin with 3 teeth excluding outer supraorbital tooth; tooth 1 low, obtuse, triangular; tooth 2 triangular or anteriorly directed; tooth 3 minute. Anterolateral angle of basal antennal segment not projecting, slightly or not entering orbital hiatus. Pterygostomial region usually without setae or with scattered short setae; inferior margin sometimes covered by setae of third maxilliped coxa. Chelae (Pl. 1E, F) unequal with tips of fingers hollowed, spoon-like; outer surface granulate with numerous setae at articulation of finger. Ambulatory (Pl. 1A) legs with sparse long, simple setae; few scattered plumose setae; extensor margin serrated, without long spines; tip of dactylus bifid; distal pigmented spine slightly shorter than curved tip. Male thoracic sternum (Pl. 1D) with press button located on sternite 5, 2/3 way to suture between sternites 4, 5. Male abdomen (Pl. 1D) long, narrow, smooth; somites 3 to 5 fused without discernible sutures except slight lateral notch on suture 4/5; somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 37A) tip truncate, pointed, with short, stout proximally-directed setae.

Remarks. This species is easily identified by the tuft of numerous setae on the external surface of the chelae at the articulation of the finger (Pl. 1E, F) (vs. no tuft in other *Chlorodiella* species). It is one of two *Chlorodiella* species, along with *Chl. cochlearis*, with only three anterolateral teeth (vs. 0, 2 or 4 in other species). The G1 morphology is distinct as well, differing from that of its congeners in having a relatively simple, truncate tip (Pl. 37A) (vs. spatulate, hooked, curved, etc. in other species except *Chl. cochlearis*) and shorter terminal setae. The G1 is perhaps closest to *Chl. cochlearis* in its relatively simple, truncate tip (Pl. 37B). Both of these species are positioned basally on the *Chlorodiella* phylogeny (Fig. 15).

Chlorodiella barbata is rather unique in that it often inhabits seaweed (pers. obs., Ward 1932, Holthuis 1953). Specimens are also commonly found in coral rubble and rocky areas usually in shallow water (< 2 m), but sometimes deeper (> 3–4 m) (pers. obs., Ward 1939, Holthuis 1953, Serène 1984).

Distribution. *Chlorodiella barbata* is known from many localities between Madagascar, Japan, the Great Barrier Reef, and French Polynesia. The species is absent from Hawaii (Pl. 46A).

Chlorodiella cochlearis (Zehntner 1894)

Pls (2, 37B, 46B)

Sphaerozius cochlearis Zehntner 1894: 151, pl. 7, fig. 5a–c [Type locality: Ambon Indonesia].

Chlorodiella corallicola Miyake & Takeda 1968: 389, figs 1–2 [Type locality: Ngarsmau, Babldáob I., Palau Is.]. — Serène 1968: 81 [List]. — Garth & Kim 1983: 687 [Romblon, between Burias and Luzon, Philippines]. — Ng, 2008: 196 [List].

Material examined. *Indonesia:* Lectotype (present designation) of *Sphaerozius cochlearis*: 1 female (4.1 × 2.6), Ambon Island, Indonesia. — 1 male, 4.2 × 2.8 (ZRC 2013.1586), Stn. BL11-014, BALI-0257, 1–3 m, hand, snorkel, under rock, sand, scattered coral, rubble, seagrass, Waha, right out front of office, Wanci, Sulawesi, Indonesia, coll. 25 June 2011.

Philippines: 2 males, larger male = 6.35 × 4.35 (ZRC 2010.0371), Stn. B2, 5 m, 9°33.0'N 123°46.5'E, reef slope, Alona Reef, Panglao Island, Philippines, coll. 31 May 2004. — 1 male, 7.45 × 5.00 (ZRC 2013.0453), Stn. B24, 38 m, 9°29.4'N 123°56.0'E, floor of cave, Pamilacan Island, Philippines, coll. 25 June 2004. — 1 male, 6.05 × 3.85 (ZRC 2010.0370), Stn. R38, 6–37 m, 9°29.4'N 123°56.0'E, reef slope, Pamilacan Island, Philippines, coll. 11

June 2004. — 1 ovigerous female, 4.3 × 2.7 (ZRC 2003.0291), Buyong Maribago, Mactan Island, Cebu, Philippines, coll. P. Clark, 30 July 2003. — 1 ovigerous female, 4.9 × 3.0 (USNM 1181259), 12 38 15 N, 122 12 30 E, Romblon Passage, Tablas Island, Roblon, Philippines, Sibuyan Sea, coll. United States Fish Commission, 25 March 1908.

Palau: 2 paratype males, 7.1 × 5.0 – 6.4 × 4.0 (KMNH 1619), 26 m, 134°33'E 7°37'N, Ngarsmau, Babldáob I., Palau Is, coll. S. Miyake, 14 July 1939.

Caroline Islands: 1 male, 4.5 × 2.7 (USNM 1181262), lagoon reef margin, western reef between Elangalap Island and the northwest end of Falarik Island, Ifalik Atoll, Caroline Islands, Yap, Micronesia, coll. D. Abbott, Pacific Science Board Survey, 20 October 1953. — 1 female, 4.0 × 2.5 (USNM 1181263), near the main pass, just inside the east spit of Ella, Ifalik lagoon, Yap Islands, Caroline Islands, Micronesia, coll. Pacific Science Board Survey, 16 October 1953. — 1 female, 4.3 × 2.6 (USNM 1181261), patch reef on lagoon bottom, approximately 1400 feet south of the northwest tip of Falarik Island, Ifalik Atoll, Caroline Islands, Yap, Micronesia, coll. R. Harry, Pacific Science Board Survey, 3 October 1953.

Guam: 1 female, 5.6 × 3.4 (USNM 1184663), Guam.

Great Barrier Reef: 1 ovigerous female, 4.80 × 3.45 (UF 17195), AUST-1300, AUST-ST-061, 17–19 m, rubble wash, coarse sand and rubble, reef base, fore reef, Day Reef, Lizard Island, Queensland, Australia, coll. N. Bruce, 19 February 2009. — 1 female, 6.30 × 4.15 (UF 17134*), AUST-1215, AUST-ST-057, 15–18 m, algae covered, fore reef, Yonge Reef, Lizard Island, Queensland, coll. C. Arango, 18 February 2009. — 1 male, 5.3 × 3.1 (UF 17346), AUST-1539, AUST-ST-072, 25–30 m, deep rubble, for reef base, Day Reef, Lizard Island, Queensland, Australia, coll. S. Smith & K. Mills, CReefs Expedition, 21 February 2009. — 1 male, 5.5 × 3.7 (UF 17367), AUST-1576, AUST-ST-072, 25–30 m, deep rubble, for reef base, Day Reef, Lizard Island, Queensland, Australia, coll. S. Smith & K. Mills, CReefs Expedition, 21 February 2009.

Vanuatu: 2 males, 3.9 × 2.6 – 5.1 × 3.3, 2 females, 4.4 × 2.9 – 5.0 × 3.1, 1 ovigerous female, 4.2 × 2.1 (ZRC 2013.1585), Stn. DB71, 7 m, 15°21.6'S, 167°12.5'E, massive coral, S Turtle Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 27 September 2006. — 1 male, 4.2 × 2.6 – 7.1 × 4.6 (ZRC 2013.1590), Stn. FP47, Vanuatu, coll. Santo Marine Biodiversity Survey, 03 October 2006. — 3 males, 5.1 × 3.2 – 5.7 × 3.6, 1 ovigerous female, 5.4 × 3.4 (ZRC 2013.1602), Stn. FB92, 2-4 m, 15°33.6'S, 167°16.6'E, muddy coral sand, Tutuba Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 14 October 2006.

Marshall Islands: 1 male, 6.4 × 4.0 (USNM 155977), Bikini Lagoone, Bikini Atoll, Ralik Chain, Marshall Islands, coll. L. Schultz, 13 April 1946.

Diagnosis. Carapace (Pl. 2B) transversely hexagonal, ca. 1.5 broad as long; dorsal surface smooth, regions poorly or undefined; anterior border of 2M with low ridge; presence of low lateral, transverse ridges posterior to orbital region and connecting to 4th anterolateral tooth. Angle formed at lateral suture of superior margin of orbit relatively less obtuse, ca.135°. Front (Pl. 2 C) broad, deflexed, lined with few narrow, long setae; submedian lobes convex, separated by shallow V-shaped notch. Anterolateral margin with 4 teeth; tooth 1 confluent with outer supraorbital tooth; teeth 1–3 anteriorly directed with pronounced, arched posterior margin; tooth 4 smallest but distinct. Anterolateral angle of basal antennal segment arched, extending ca. halfway into short orbital hiatus. Pterygostomial region without setae. Major chela robust with relatively stout dactylus. Ambulatory (Pl. 2A) legs with sparse long, simple setae; extensor margin of merus serrated; tip of dactylus bifid; distal pigmented spine slightly shorter than curved tip. Male thoracic sternum (Pl. 2D) with press button located on sternite 5, almost touching suture between sternites 4, 5. Male abdomen (Pl. 2D) long, broad; somites 3 to 5 fused, sutures not discernible; somite 6 broader than long; telson slightly longer than broad. G1 (Pl. 37B) tip truncate, rounded with short, stout, proximally-directed setae.

Remarks. *Chlorodiella cochlearis* has had a complicated history. Originally placed in the genus *Sphaerozius* by Zehntner (1894), Odhner (1925) moved the species to *Chlorodius* without explanation. Subsequently, the species name has not been used. Two types were designated in the original description. Both are females from Ambon, Indonesia and, as it turns out, are two different species. The two specimens are small and rather similar. However, they differ in two key features: the anterolateral teeth and depressions of the carapace. In his description, Zehntner (1894) stated that the *Sphaerozius cochlearis* has four anterolateral teeth, including the outer supraorbital tooth which is rather prominent. He also stated that among the depressions in the dorsal carapace are: 1) a mesial longitudinal groove leading from the front; 2) a transverse groove intersecting the longitudinal groove on the hepatic region; 3) a slight transverse furrow behind the front and orbits; and 4) a low transverse furrow of the branchial regions. These characters are only present in one of the syntypes. The other syntype has 5 anterolateral teeth, including the outer supraorbital tooth, and lacks these depressions. Zehntner's (1894) description and corresponding syntype were compared with the paratypes of *Chlorodiella corallicola* Miyake and Takeda, 1968, and were determined to be conspecific (Miyake & Takeda 1968: fig. 1). This specimen is presently designated as the lectoype. *Chlorodiella corallicola* is regarded as a junior subjective synonym of *Chl. cochlearis* (Zehntner, 1894). The identity of the other syntype is unknown. The specimen is a small juvenile, and is thus very difficult to identify. It is certainly not *Chl.*

quadrilobata or *Chl. ohshimai*, as the specimen has four anterolateral teeth, excluding the outer supraorbital tooth (versus four lobes, and one lobe and one sharp, anteriorly directed tooth in *Chl. quadrilobata* and *Chl. ohshimai*, respectively). It is also unlikely to be *Chl. barbata*, as the specimen lacks the brush of setae on the exterior of the chelar palm (characteristic of *Chl. barbata*). Due to the size of the specimen, it is difficult to determine which of the remaining species (*Chl. xishaensis*, *Chl. cytherea*, *Chl. laevissima*, *Chl. martensi*, *Chl. planapexa* sp. nov., and *Chl. nigra*) it is.

Chlorodiella cochlearis is easily distinguished from its congeners by its anterolateral teeth (Pl. 2B). Tooth 1 is very prominent and confluent with the outer supraorbital tooth (vs. absent or low in other species). Furthermore, teeth 2 and 3 are very pronounced and have a diagnostic shark-fin-like shape due to the arc of their posterolateral margins. *Chlorodiella cochlearis* is perhaps closest to *Chl. barbata* in having a relatively broad carapace and orbits, and truncated G1s with short setae (Pls 1B, 2B, 37A, B). However, these two species differ in the above features and, in *Chl. cochlearis*, the absence of setae on the external surface of the chelae at the articulation of the dactylus (Pl. 2E, F) [versus with a brush of setae in *Chl. barbata* (Pl. 1E, F)].

This species is found in coral reef areas and has been collected from depths between 1 to 30 m.

Distribution. *Chlorodiella cochlearis* occurs in the Coral Triangle (type locality = Ambon, Indonesia) and adjacent areas: Palau, Guam, and the Great Barrier Reef. *Chlorodiella cochlearis* also is reported from the central and southern Pacific from Vanuatu to the Caroline Islands, Micronesia and Bikini Atoll, Marshall Islands. It is not known from the Indian Ocean, French Polynesia, or the Hawaiian Islands (Pl. 46B).

Chlorodiella cytherea (Dana, 1852)

Pls (3, 37C)

Chlorodius cytherea Dana 1852a: 79 [type locality: Tuamotu Archipelago, Tahiti, Hawaii]; 1852b: 213, pl. 12, fig. 2a [Raraka, Tuamotus; Tahiti; Hawaiian Islands]; 1855: pl. 12, fig. 2 a–c. — Stimpson 1858: 31; 1907: 50 [Hawaiian Is.; Ousima].

Pilodius martensi Nobili 1906c: 268 [Red Sea]. — Stebbing 1910: 300 [List].

Chlorodiella cytherea Ward 1939: 11 [Savaii Island, Samoa]. — Forest & Guinot 1961: 95, fig. 90–92, 98 a, b [Hikueru, Tuamotu Islands; Tahiti]. — Guinot 1962b: 238 [Fadiffolu Atoll, Maldives]; 1964b: 70 [Abulat, Saudi Arabia; Djibouti]; 1967c: 262 (part) [List]. — Michel 1964: 24 [Mauritius]. — Serène 1968: 81 [List]; 1984: 259, fig. 169, pl. XXXVI C [Nosy Be, Tulear and Fort-Dauphin, Madagascar; Mayotte, Iles Comoros]. — Garth 1973: 320 [Maldives, Sri Lanka]. — Serène *et al*. 1976: 18 [Ambon I., Indonesia]. — Takeda & Nunomura 1976: 74 [Guadalcanal (Honiala), Solomon Is.; North Island, Torres]. — Sakai 1976: 466, pl. 166, fig. 2 [Yoron I., Ishigaki I., and Taketomi I., Japan]. — Takeda & Miyake 1976: 108 [Ogasawara Is., Japan]. — Takeda & Kurata 1977: 94 [Ogasawara Is., Japan]. — Peyrot-Clausade 1977a: 26 [Tulear, Madagascar]; 1977b: 213 [Moorea]; 1989: 112 [Tikehau, Tuamotu]. — ?Chen & Lan 1978: 270; fig. 5, 7 (1-3), pl. 2, fig. 5 [Xisha Islands]. — Ribes 1978: 126 [Reunion I.]. — Thomassin 1978: 64 [Tulear, Madagascar]. — Dai *et al*. 1986: 316, pl. 45(6), fig. 169(4) [Review]. — Titgen 1987: 107, fig. 1a-d [Hawaii]. — Holthuis 1953: 14 [Saipan; Bikati Island and Onotoa, Gilbert Islands]. — Peyrot-Clausade 1989: 112 [Tikehau, Tuamotu]. — Dai & Yang 1991: 340, pl. 45(6), fig. 169(4) [Review]. — DeFelice *et al*. 1998: 16 [Midway Atoll, Hawaiian Is.]. — DeFelice *et al.* 2002: 72 [List]. — Davie 2002: 519

[Elizabeth and Middleton reefs, Tasman Sea, Australia]. — Coles *et al*. 2002a: 269, 333 [Oahu]. — Godwin & Bolick 2006: 39, 49 [Honolulu, Hawaiian Is.]. — Coles & Swensen 2010: 87 [List].

Chlorodiella davaoensis Ward 1941: 10, figs 17, 18 [Gulf of Davao, Philippines]. — Serène 1968: 81 [List].

Chlorodiella niger, Rathbun 1906: 857 [Hawaiian Islands] (part). — Edmondson 1923b: 1550, 1552 [H.I., Kure Atoll]; 1925: 44 (part) [Hawaiian Is.]; 1933: 249 [Review]; 1962a: 281, fig. 23d [Hawaiian Is.]. — Pesta 1933: 280 [Hawaiian Is.]. — Coles, DeFelice & Eldredge 1999: 159 [O'ahu]. — ?Coles, Reath, Longenecker, Bolick & Eldredge 2004: 143 [Hawaiian Is.]. — ?Coles *et al.* 2008: 62, 69 [Hawaiian Is.]. (not *Cancer niger* Forskål, 1775)

Chlorodiella niger var. *cytherea*, Laurie 1915: 449 [Sudan, Red Sea]. [not *Chlorodiella nigra* Dana, 1852]

Chlorodiella nigra, Edmondson 1946: 296 [Hawaiian Is.]. — Coles *et al*. 2004: 143 [Maui, Hawaii]. — Coles *et al.* 2008: 62, 69 [Oahu and Molokai, Hawaiian Is.]. (not *Cancer niger* Forskål, 1775)

Eurüppelia sp. Cano 1889b: 209 [O'ahu].

(?) *Chlorodiella laevissima* Miyaké, 1938: 192, fig. 3b [Taiwan].*Chlorodiella crispipleopa* Dai, Yang, Song & Chen 1986: 317, pl. 45(7), fig. 169(1) [Xisha Is.; Taiwan]. — Dai & Yang 1991: 341, pl. 45(7), fig. 169(1) [Xisha Is.; Taiwan]. — Ng *et al.* 2008: 196 [List].

Material examined. *Saudi Arabia:* Holotype male, 7.5 × 5.0 (UF 36830*), Stn. SAFA-016, 18.07308° 40.8859°, 7–9 m, in rubble, fore reef wall and barrier reef flat, offshore of Farasan Banks, Shib Radib, Saudi Arabia, coll. A. Anker *et al.*, 8 March 2013. — 1 female, 5.4 × 3.6 (UF 33020*), Stn. DJRS-035, 22.26455° 39.0263°, 1–20 m, seaward reef slope and front of shelf reef, Thuwal, Abu Gishaa, Saudi Arabia, coll. G. Paulay, 8 October 2012. — 1 female, 5.9 × 3.8 (UF 33007*), Stn. DJRS-039, 22.2740833333333° 39.0512°, 2–20 m, seaward reef slope & front of shelf reef, Thuwal, Saudi Arabia, coll. M. Berumen & G. Paulay, 10 October 2012. — 1 female, 5.4 × 3.4 (UF 36679), Stn. SAFA-008, 18.22055° 41.32438°, 8 m, in rubble, reef bank, Farasan Banks, Marca Island, Saudi Arabia, coll. A. Anker *et al.*, 6 March 2013. — 1 male, 6.8 × 4.4 (UF 36545), Stn. SAFA-006, 18.65952° 40.82697°, 1–2 m, under rock, fringing reef, Farasan Banks, Pelican (Ablo) Island, Saudi Arabia, coll. A. Anker *et al.*, 5 March 2013. — 1 male, 6.7 × 4.6 (UF 37295*), Stn. SAFA-002, 19.5707° 40.00878°, 2–20 m, reef lagoon and fore reef wall, Farasan Banks, Shi'b Ammar, Saudi Arabia, coll. A. Anker *et al.*, 3 March 2013. — 1 male, 5.6 × 3.6 (UF 36148), Stn. SAFA-005, 19.00533° 40.14815°, 1–7 m, in *Tubipora* rubble, reef lagoon and barrier reef flat, offshore of Farasan Banks, Dolphen Lagoon, Saudi Arabia, coll. A. Anker *et al.*, 4 March 2013.

Djibouti: 1 female, 7.8 × 5.1 (UF 33090*), Stn. DJRS-006, 11.973667° 43.335833°, 4–6 m, reef slope, NE Gulf of Tadjoura, E of Obock, Djibouti, coll. G. Paulay, 28 September 2012.

Madagascar: 1 male, 6.4 × 4.3 (UF 14355*), Stn. MGNW-23, -13.4139° 48.3056°, 1–6 m, rubble, seagrass flat and adjacent sand/reef slope, Nosy Be, across bay from CNRO complex, off Lokobe Reserve, Madagascar, coll. G. Bakary *et al*., 16 May 2008.

Christmas Island: 1 male, 12.0 × 7.0 (ZRC 2010.0373*), CI-31(185), Christmas Island, coll. 2 February 2010. — (?) 2 males, 8.2 by 5.2 mm – 6.8 by 4.3 mm, 2 females, 6.7 by 4.2 mm – 5.2 by 3.4 mm (ZRC 2013.1559), Stn. CI-17-2011, Christmas Island, 2011.

Spratly Islands: 6 males, 7.07 × 5.23 – 11.77 × 8.12 (IOCAS XXX708), Spratly Islands. — 44 males and 53 females, 6.72 × 4.18 – 12.17 × 7.25 (IOCAS XXX695), Spratly Islands.

Australia: 1 male, 10.4 × 6.8 (ZRC 2010.0372), NING 0033, NR10-004, 6 m, -22.67861 113.6425, snorkel and SCUBA, in rubble, bommies on sand, dead and live coral, edge in Front of Ningaloo Station, Ningaloo Reef, Western Australia, coll. CReefs Expedition, R. Lasley & S. Nguyen, 15 May 2010. — 1 female, 8.5 × 9.7 (UF 25986*), Stn. HI09-120, -23.54463° 151.76234°, 1–3 m, Heron Island, Queensland, Australia, coll. R. Lasley, 27 November 2009. — 1 male, 10.1 × 6.5 (UF 24791), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinnacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 male, 9.1 × 5.8 (UF 25444*), Stn. HI09-131, -23° 152°, Heron Island, Queensland, Australia, coll. November 2009. — 1 male, 10.4 × 6.7 (UF 24914*), Stn. HI09-019, -23.43135° 152.03375°, 1–2 m, under rock, reef crest, reef flat, Heron Island, Sykes Reef, Queensland, Australia, coll. F. Michonneau & R. Lasley, 14 November 2009. — 1 male, 7.7 × 5.0 (UF 25630), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009. — 1 female, 8.8 × 5.8 (UF 24891*), Stn. HI09-019, -23.43135° 152.03375°, 1–2 m, under rock, reef crest, reef flat, Heron Island, Sykes Reef, Queensland, Australia, coll. F. Michonneau & R. Lasley, 14 November 2009. — 1 female, 5.8 × 4.0 (UF 25546*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009. — 1 ovigerous female, 7.6 × 5.0 (UF 25224), Stn. HI09-041, -23.4732833° 151.9504667°, Heron Island, Queensland, Australia, coll. 17 November 2009. — 1 male, 10.8 × 7.1 (UF 24965*), Stn. HI09-017, -23.43211667° 152.03375°, 15–25 m, in rubble, steep outer slope, Heron Island, Sykes Reef, Queensland, Australia, coll. S. McKeon, 14 November 2009. — 1 female, 7.9 × 5.1 (UF 25523*), Stn. HI09-076, -23.4331667° 151.9170833°, 6–16 m, mostly under rocks, outer reef, Heron Island, North Heron, Queensland, Australia, coll. 22 November 2009. — 1 male, 9.9 × 6.3 (UF 25552*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009. — 1 female (damaged) (UF 22616*), Stn. NIN09-St-89, -22.76912° 113.7046°, 12 m, in rubble, Ningaloo Reef, Western Australia, Australia, coll. J. Caley, May 2009. — 1 male, 11.4 × 7.3 (UF 22470*), Stn. NIN09-St-71, -22.62317° 113.6532°, 6–7 m, in rubble, back reef, patches of live corals and rubble on sand, Ningaloo Reef, Norwegian Bommies, Western Australia, Australia, coll. F. Michonneau, May 2009. — 1 male, 4.9 × 3.4 (UF 22475*), Stn. NIN09-St-71, -22.62317° 113.6532°, 6–7 m, in rubble, back reef, patches of live corals and rubble on sand, Ningaloo Reef, Norwegian Bommies, Western Australia, Australia, coll. F. Michonneau, May 2009. — 1 male, 6.7 × 4.5 (UF 22164*), Stn. NIN09-St-55, -23.05463° 113.8221°, 0–1 m, under rock, rocky intertidal, relatively exposed, Ningaloo Reef, S of Ningaloo Station, Western Australia, Australia, coll. R. Lasley & F. Michonneau, May 2009. — 1 female, 11.5 × 7.2 (UF 22472*), Stn. NIN09-St-71, -22.62317° 113.6532°, 6–7 m, in rubble, back reef, patches of live corals and rubble on sand, Ningaloo Reef, Norwegian Bommies, Western Australia, Australia, coll. F. Michonneau, May 2009. — 1 male, 12.8 × 8.0 (UF 21516*), Stn. NIN09-St-7, -22.74152° 113.6836°, 2–3 m, in rubble, back reef, patchy corals on sand, Ningaloo Reef, S shallow bommies, Western Australia, Australia, coll. R. Lasley, 15 May 2009. — 1 male, 7.8 × 5.3 (UF 21815*), Stn. NIN09-St-29, -22.61943° 113.641°, 3–6 m, under rock, patch reefs in lagoon, Ningaloo Reef, Norwegian Bommies, Western Australia, Australia, coll. R. Lasley, May 2009.

Indonesia: 1 female, 5.8 × 3.9 (ZRC 2013.1699*), Stn. BL11-002, BALI-0026, 0–10 cm, -8.713480555555 115.251575, hand, intertidaling, under rock, hard exposed substrate with sandy patches, scattered coral, exposed (low tide), closest beach from Rama Villas, Sanur Beach, Bali, Indonesia, coll. 15 June 2011.

Philippines: holotype male, 10mm (AMNH 8364) Western Coast of Gulf of Davao, Davao Island, Philippines, coll. Oesch during the months March to July, 1936 or Dr. Willard G. Van Name in November 1937. — 3 males (largest = 9.12 x 6.12), 8 females (AMNH 7818), Gulf of Davao, Philippine Islands, 9 May 1936. — 7 males (largest = 9.55 x 6.63), 2 females (AMNH 7816), Gulf of Davao, Philippine Islands, 9 May 1936. — 1 male, 8.23 x 5.40, 2 females (AMNH 8082), Gulf of Davao, Philippines, 9 May 1936. — 1 male, 8.20 x 5.42 (AMNH 8579), Gulf of Davao, Philippines, 14 November 1947. — 1 male, 9.6 × 6.2, 2 females, 8.6 × 5.6 – 9.6 × 6.0 (ZRC 2008.0644*), night dive, reef flat, Alona Beach, Panglao Island, Philippines, coll. H. Tan & P. Clark, 25 July 2003. — 1 male, 3.8 × 2.6, 2 females, 4.7 × 3.2 – 6.2 × 4.1, 1 ovigerous female, 5.6 × 3.6 (ZRC 2013.1595), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, coll. the Panglao Marine Biodiversity Project, 7 June 2004. — 1 male, 6.0 × 4.0 (ZRC 2013.1563), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, Philippines, coll. Panglao Expedition, 7 Jun 2004.

Japan: 1 male, 10.8 × 7.3 (UF 26795), Stn. GUOK10-St-051, 26.406339° 127.844547°, 0–8 m, sheltered, shallow bay, fairly silty, Okinawa, Konbu Beach to Tengan Pier, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al*., 29 June 2010. — 1 male, 4.2 × 2.8 (UF 26921), Stn. GUOK10-St-066, 24.439976° 123.776883°, 17 m, in coral rubble, fore reef, Iriomote, Hoshisuna Beach, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 10 July 2010. — 1 male, 7.8 × 4.2 (UF 7211*), BOKI-12, 0–0.1 m, 26°51.803'N 128°15.863'E, reef flat, Kunigami Bay just SE of Cape Hedo, Okinawa, Japan, coll. G. Paulay *et al*., 3 July 2004.

Mariana Islands: 3 males, 5.3 × 3.1 – 6.2 × 3.8 (UF 4013*), GP-Loc-752, 0–1 m, 13.4245° 144.7858°, under rocks, outer reef flat, N Pago Bay, Guam Island, Mariana Islands, coll. G. Paulay, May 2003. — 1 male, 9.5 × 5.9 (UF f/2912), ZZZ-087499, 1–3 ft, among coral rubble and rocks, NE side, Alutom Islet, Guam Island, Mariana Islands, coll. H. Conley, 6 June 2002. — 2 males, 5.7 × 3.5 – 7.3 × 4.4 (UF 391*), BGUAM-080-4, 4–8 ft, fore reef, under rubble in surge channels and pockets, Pago Bay, Guam, Mariana Islands, coll. G. Paulay, 14 August 2000. — 1 male (damaged) (UF 1979*), ZZZ-086651, 10–20 ft, among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 12 March 2002. — 2 males, 10.5 × 6.6 – 11.5 × 7.4 (UF 2912*), ZZZ-087499, 1–3 ft, among coral rubble and rocks, NE side, Alutom Islet, Guam Island, Mariana Islands, coll. H. Conley, 6 June 2002. — 1 male, 7.7 × 4.7 (UF 2804*), ZZZ-087476, 2–4 ft, among rocks and coral, NE Side, Alutom Islet, Guam Island, Mariana Islands, coll. H. Conley, 22 April 2002. — 1 female, 6.2 × 3.9 (UF 2922*), ZZZ-087556, 10–15 ft, among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 30 May 2002. — 1 male, 8.1 × 5.0 (UF 1990*), ZZZ-086662, among rocks, intertidal, E of Camel Rock, Hospital Point, Asan Bay, Guam Island, Mariana Islands, USA, coll. H. Conley, 18 March 2002. — 2 males, 7.0 × 4.3 – 7.1 × 4.6, 1 ovigerous female, 5.8 × 3.6 (UF 1304*), ZZZ-085736, 15–25 ft, among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 22 Aug 1984. — 1 male, 6.2 × 3.9 (UF 2061*), ZZZ-086651, 10–20 ft, among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Island, Mariana Island, coll. H. Conley, 12 March 2002. — 6 males, 5.8 × 3.7 – 7.7 × 4.5, 1 female, 5.5 × 3.5 (UF 1256*), ZZZ-085731, 10–20 feet, among rocks, near harbor entrance, glass breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 22 August 1984.

Caroline Islands: 1 female, 6.8 × 4.2 (UF 5278), JAS-PON-063, 0–1 m, 6.758° 157.995°, reef flat, rock, entry channel to inner lagoon, Ant Atoll Channel, Ant Atoll, Caroline Islands, Federated States of Micronesia, coll. J. Starmer, 12 March 2003.*New Caledonia:* 1 ovigerous female, 7.6 × 4.6 (UF 37973*), NewC13-553, NEST21, 0–3 m, -17.9121° 162.899°, rubble field, lots of *Xenia* and algae, some live coral, N tip, Huon Atoll, New Caledonia, coll. N. Evans, 13 November 2013.

Vanuatu: 1 male, 6.4 × 3.9 (ZRC 2013.1700*), Stn. VM54, 15°28.9'S, 167°15.5'E, intertidal, E Palikulo Peninsula, Vanuatu, coll. Santo Marine Biodiversity Survey, 08 October 2006. — (?) 1 male, 8.1 × 5.0 (ZRC 2013.1564), Stn. VM58, intertidal, 15°28.6'S, 167°15.3'E, soft and hard bottom, Palikulo Peninsula, Vanuatu, coll. Santo Marine Biodiversity Survey, 07 October 2006. — (?) 2 males, 8.1 × 4.9 – 6.7 × 3.0, 1 female, 5.9 × 3.5 (ZRC 2013.1565), Stn. VM35, intertidal, 15°29.4'S, 167°15.2'E, soft bottom, Palikulo Peninsula, Vanuatu, coll. Santo Marine Biodiversity Survey, 24 September 2006.

Wake Island: 1 male, 8.7 × 5.3 (UF 36087*), Stn. Kim-WAK-St-14, 19.3 166.7, 0 m, under rubble, ocean side of atoll, Wake Island, USA, coll. S. Kim, 26-3-2009.

Marshall Islands: 1 female, 7.7 × 4.7 (UF 13428*), FM-MAJ08-159, FM-St-MAJ08-11, 0 m, 7.1579° 171.2144°, intertidal rocks and pools, channel (east end of island), Kolalen, Marshall Island, Republic of the Marshall Islands, coll. F. Michonneau & S. Kim, 8 April 2008.

Cook Islands: 1 male, 6.8 × 4.3 (UF 11713*), MRARO-01.7, MRARO-001, 0–5 ft, -21.2333° -159.7667°, snorkel, reef flat, in front of Teina's brother's house, Vaima'anga (S coast) near Captain Cook Resort, Rarotonga Island, Cook Islands, coll. M. Malay, 23 June 2006. — 1 female, 6.8 × 4.1 (UF 13221*), MRARO-01.10, MRARO-001, 0–5 ft, -21.2333° -159.7667°, snorkel, reef flat, in front of Teina's brother's house, Vaima'anga (S coast) near Captain Cook Resort, Rarotonga Island, Cook Islands, coll. M. Malay, 23 June 2006. — 1 male, 6.4 × 3.9 (UF 11715*) MRARO-01.8, MRARO-001, 0–5 ft, -21.2333° -159.7667°, snorkel, reef flat, in front of Teina's brother's house, Vaima'anga (S coast) near Captain Cook Resort, Rarotonga Island, Cook Islands, coll. M. Malay, 23 June 2006. — 1 male, damaged specimen (UF 1360*), KIKAO, 0–2 m, Nikao, Rarotonga Island, Cook Islands, coll. C. Meyer, 18 October 2001. — 1 female, 5.7 × 3.5 (UF 11717*), MRARO-01.18, MRARO-001, 0–5 ft, -21.2333° -159.7667°, snorkel, reef flat, in front of Teina's brother's house, Vaima'anga (S coast) near Captain Cook Resort, Rarotonga Island, Cook Islands, coll. M. Malay, 23 June 2006. — 1 male, 6.0 × 3.8 (UF 11711*) MRARO-01.5, MRARO-001, 0–5 ft, -21.2333° -159.7667°, snorkel, reef flat, in front of Teina's brother's house, Vaima'anga (S coast) near Captain Cook Resort, Rarotonga Island, Cook Islands, coll. M. Malay, 23 June 2006.

Hawaiian Islands: 1 male, 9.8 × 6.2 (UF 8763*), BOAHU-134, GP-Loc-855, 0 m, 21.4353° -157.7888°, under rocks in mid intertidal, inner reef flat, Coconut Island, Kaneohe Bay, Oahu Island, Hawaiian Islands, coll. C. Meyer *et al*., 2 March 2006. — 2 males, 8.5 × 5.3 – 11.1 × 7.1, 1 female, 10.4 × 6.3, 1 ovigerous female, 9.7 × 6.1 (UF 8737*), BOAHU-127, GP-Loc-855, 0 m, 21.4353° -157.7888°, under rocks in mid intertidal, inner reef flat, Coconut Island, Kaneohe Bay, Oahu Island, Hawaiian Islands, coll. C. Meyer *et. al*., 2 March 2006. — 1 female, 8.6 × 5.2 (UF 12144*), BFFS-550, FFS-0086, 4 ft, 23.8732° -166.2348°, rubble brushing, reef crest, French Frigate Shoals, Hawaiian Islands, B. Zgliczynsky *et al*., 16 October 2006. — 1 male, 6.4 × 4.1

(UF 3783*), CP-G-2003-012, 20.8108° -156.6214, intertidal on cobble beach, Hekili Point, Maui, Hawaii, coll. C. Pitman, 29 March 2003. — 1 ovigerous female, 5.8 × 3.8 (UF 12145*), BFFS-550, FFS-0086, 4 ft, 23.8732° -166.2348°, rubble brushing, reef crest, French Frigate Shoals, Hawaiian Islands, B. Zgliczynsky *et al.*, 16 October 2006. — 1 male, 8.1 × 5.1 (UF 12341*), BFFS-1251, FFS-0091, 15 ft, 23.8733° -166.2347°, rubble extraction, back reef, French Frigate Shoals, Hawaiian Islands, coll. R. Brainard & B. Zgliczynski, 16 October 2006. — 1 male, 7.7 × 4.6 (UF 12332*), BFFS-1242, FFS-0091, 15 ft, 23.8733° -166.2347°, rubble extraction, back reef, French Frigate Shoals, Hawaiian Islands, coll. R. Brainard & B. Zgliczynski, 16 October 2006.

Society Islands: 1 female, 8.1 × 5.1 (UF 9853*), BMOO-1188, GP-Loc-878, 0–2 m, -17.4982° -149.8638°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at northwest side of Opunohu Bay, Moorea Islands, Society Islands, French Polynesia, coll. C. Lydeard, C. Meyer, 13 July 2006. — 1 male, 6.5 × 4.0 (UF 1607*), BM00-033, 0–2 m, under rocks, southern end of narrow fringing reef before it widens, Pt. Faaupo, coll. G. Paulay, 30 October 2001. — 1 male, 9.9 × 6.2 (UF 10000*), BMOO-481, GP-Loc-862, 0-1 m, -17.4964° -149.7528°, by hand, under rock in 10–20cm sand in horizontal burrow, narrow oceanic reef flat, narrow reef flat around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. C. McKeon & G. Paulay, 20 June 2006. — 1 male, 6.3 × 4.0, 4 females, 5.5 × 3.5 – 7.4 × 4.7 (UF 9852*), BMOO-1189, GP-Loc-878, 0–2 m, -17.4982° -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll., C. Lydeard & C. Meyer, 13 July 2006. — 1 ovigerous female, 5.6 × 3.4 (UF 9697*), BMOO-726, GP-Loc-874, 0–2 m, -17.4772° -149.8306°, by hand, under rocks, 1–60 m of reef crest, outer part of barrier reef, barrier reef between Cook's and Opunohu bays (Vaipahu), Moorea Island, Society Islands, coll. C. McKeon & G. Paulay, July 2006. — 1 male, 4.9 × 3.2 (UF 24262*), Stn. BIZ-257, -17.59568° -149.84564°, 0.5–1 m, under and on rocks and rubble, inside barrier reef, near pass channel, Atiha Bay, inside barrier reef, on west side of pass, Moorea Island, Society Islands, French Polynesia, coll. S. McPherson *et al*., 8 December 2009.

Tuamotu Islands: 1 male, 7.9 × 4.9, 1 female, 6.6 × 4.0 (UF 1676*), BRNG-032, -14.9833° -147.6167°, nestled in crevices in reef rock, outer reef flat and reef crest, off far W Hoa, Avatoru Motu, Rangiroa Atoll, Tuamotu Archipelago, coll. G. Paulay, 19 October 2001. — 1 male, 9.4 × 5.4 (UF 1660*), BTIK-001, 0–3 m, -15.1333° -148.2333°, under rocks, fringing reef and sand flat, lagoon fringing reef and sand flat in front to Aito Motel, Tuherahera, Tikehau Atoll, Tuamotu Archipelago, coll. G. Paulay, 10 June 2001. — 1 male, 9.0 × 5.7 (UF 1665*), BRNG-032, -14.9833° -147.6167°, nestled in crevices in reef rock, outer reef flat and reef crest, off far W Hoa, Avatoru Motu, Rangiroa Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 20 October 2001.

Diagnosis. Carapace (Pl. 3B) transversely hexagonal, ca. 1.6 broad as long; surface appearing smooth without magnification, minutely granulate, granules sometimes more discernible laterally; 2L, 3L, 4L elevated, sometimes as ridges, separated by broad grooves, elevations sometimes indiscernible especially in small specimens; 3M poorly defined; remaining regions poorly or undefined. Front (Pl. 3C) broad; submedian lobes slightly convex, double rimmed, minutely granulate, separated by shallow V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 near and similar in size to outer supraorbital tooth; tooth 2 broad, large, slightly anteriorly directed; tooth 3 large, acute, anteriorly directed, tip sharp; tooth 4 small or minute, laterally directed, forming short transverse ridge. Anterolateral angle of basal antennal segment not produced, mostly hidden behind inner suborbital projection. Pterygostomial region with plumose setae diagonally from posterior to lateral surface. Chelae (Pl. 3E, F) unequal with tips of fingers hollowed, spoon-like; major chela robust, fingers gaping. Ambulatory legs (Pl. 3A) with long, plumose setae; extensor margin of merus serrated or lined with short, distally directed spines; tip of dactylus bifid; distal pigmented spine approximately equal to curved, downward pointing tip. Male thoracic sternum (Pl. 3D) with press button located on sternite 5, slightly closer to suture between sternites 4, 5 than 5, 6. Male abdomen long, moderately broad; somites 3 to 5 fused, sutures not discernible; somite 6 ca. broad as long; telson subtriangular, slightly longer than broad. G1 (Pl. 37C) tip lined with several long, stout, simple setae on ventral surface; apex ultimately directed dorsally to laterally—i.e., "hooked" to "curled".

Remarks. Dana (1852) described *Chlorodiella cytherea* from Tuamotu, Tahiti, and the Hawaiian Islands but did not designate a holotype. His types were subsequently lost. Later, Alcock (1898: 160) synonymized *Chl. cytherea* with *Chl. nigra* without any supporting remarks. Then, he name was used as a variety of *Chl. nigra* by Larrie (1915: 449)—i.e., "*Chlorodiella nigra* var. *cytherea*". Later, Ward (1939: 11) mistakenly synonymized *Chl. laevissima* with *Chl. cytherea*, but he used the name, *Chl. cytherea*, again in 1941 (p. 10). Although, it is uncertain what species he examined. Forest & Guinot (1961), pointed out Ward's error, officially resurrecting the name *Chlorodiella cytherea*, although *Chl. laevissima* specimens were identified as such by several authors between Ward's (1939) synonymy and Forest & Guinot's (1961) correction (Lin 1949, Tweedie 1950b, Holthius 1953).

There are three contentious names to consider with respect to synonymy of *Chl. cytherea*: *Pilodius martensi*, *Chl. davaoensis* and *Chl. crispipleopa*. Nobili (1906) identified three specimens from the Red Sea as

"*Pilodius martensi*", stating that they perfectly agree ("*s'accordent parfaitement*") with Krauss' (1843) description of *Menippe martensi*. Nobili considered the species to be congeneric with the two *Pilodius* species listed in the same manuscript; these were *P. armiger* (= *Liocarpilodes armiger* Nobili, 1905) and an undetermined species. He wrote a lengthy description of his "*P. martensi*" specimens. Thus, the combination *Pilodius martensi* was born (vs. *Menippe martensi* Krauss, 1843). Later, Odhner (1925) stated his belief that *Menippe martensi* belongs to the genus *Chlorodius*, in contrast to *Pilodius*, and that Krauss' *Menippe martensi* types were likely young specimens of *Chlorodius nigra* [= *Chlorodiella nigra* (Forskål, 1775)]. However, Forest & Guinot (1961, p. 103) stated that *Menippe martensi* is actually a junior synonym of *Chlorodiella laevissima* (Dana, 1851), based on Krauss' figures. They also stated that Nobili's (1906) specimens were not *Chlorodiella nigra*, but were *Chlorodiella cytherea*. In summary, two different species (*Chl. laevissima* and *Chl. cytherea*) were described as "martensi" and placed in two genera: *Pilodius* and *Menippe*. This is reflected in Ng *et al*.'s (2008) catalog with *Pilodius martensis* Nobili, 1905 and *Menippe martensi* Krauss, 1843 listed as junior synonyms of *Chlorodiella cytherea* and *Chlorodiella laevissima*, respectively (but see resurrection of *Chl. martensi* in remarks of that species). Therefore, *P. martensis* (Nobili, 1905) is regarded as a junior synonym of *Chl. cytherea*.

In their description of *Chl. crispipleopa*, Dai *et al*. (1986) differentiated between it and *Chl. cytherea* by the elevation of the lateral regions of the carapace (costate elevations in *Chl. cytherea* versus low elevations in *Chl. crispipleopa*), shape and denticulation of the front (convex, without denticles in *Chl. cytherea* versus truncate with denticles in *Chl. crispipleopa*), shape of the second anterolateral tooth (obtusely dentiform in *Chl. cytherea* and nearly triangular in *Chl. crispipleopa*), and G1 morphology (hooked in *Chl. cytherea* and curled in *Chl. crispipleopa*). However, all of these features vary in *Chl. cytherea*—most notably, the G1 morphology. For example, two specimens of similar size from the Cook Islands (UF 11715 and UF 11711) have curled and hooked G1 tips, respectively. Therefore, *Chl. crispipleopa* is regarded as a junior synonym of *Chl. cytherea*.

Similarly, *Chl. davaoensis* is indistinguishable from *Chl. cytherea* in the aforementioned characters. In the original description, Ward (1941) only compared the species to *Chl. hirtipes* (= *Chl. nigra*). However, examination the holotype specimen has revealed that the species is conspecific with *Chl. cytherea*. This specimen has the “curled” G1 morphology.

Specimens of *Chl. cytherea* are most morphologically similar to members of the *Chlorodiella laevissima* complex in general habitus (see Remarks for *Chl. laevissima*). In fact, they have often been confused in the historical literature (see synonymies of each species). The former species is most readily distinguished from members of the *Chl. laevissima* complex by its hooked or curled G1 tip (Pls 37C, D, 38A, B) [versus spatulate or pointed in *Chl. laevissima* complex (Pls 38D, E, 39A)] and presence of setae on the pterygostomial region (versus no setae in *Chl. laevissima* complex). *Chlorodiella cytherea* has been recorded inhabiting intertidal and rock platform with pools (Serène 1984). They are also common in coral rubble.

Distribution. *Chlorodiella cytherea* is recorded from the Madagascar and the Red Sea to the Hawaiian Islands and French Polynesia.

Chlorodiella planapexa sp. nov.

Pls (8, 38C, 46D)

Chlorodius laevissimus ?Calman 1909: 705 [Christmas Island]. — ?Lenz 1910: 550 [Mananara, Madagascar].

Chlorodiella laevissima ?Miyake 1936: 508 [Yaeyama, Japan]. — ?Tweedie 1950b: 120 [Cocos Keeling Islands]. — ?Sankarankutty 1962: 136, figs. 32-33 [Niell Island, Car Nicobar]. — ?Kensley 1970: 107, fig. 3 a-d [Inhambane, Mozambique]; 1981: 44 [Mozambique]. — Dai *et al*. 1986: 319, fig. 170, pl. 46(1) [Review]. — Dai & Yang, 1991: 343, fig. 170, pl. 46(1) [Review]. — Chen & Lan 1978: 268–269: figs 2, 7 (12–13) [Xisha Islands].

Material examined. *Madagascar:* 1 male, 6.9 × 4.3 (UF 14295*), NBE-1363, MGNW-21, 4m, -13.4244° 48.3642°, broken reef, rubble, sand on shallow slope, extracted from large dead *Porites rus*, off ENE side of Nosy Vorona, Madagascar, coll. A. Anker *et al.*, 15 May 2008. — 1 male, 7.1 × 4.7, 1 ovigerous female, 6.8 × 4.3 (UF 16576*), Stn. MGNW-21, -13.4244° 48.3642°, 4 m, in dead *Porites rus*, off ENE side of Nosy Vorona, Madagascar, coll. G. Paulay *et al*., 15 May 2008.

Scattered Islands: 3 males, 3.3 × 2.3 – 3.9 × 2.6, 3 juveniles (UF 20744*), Stn. JDNO-16, -17.02221667° 42.68945°, 7 m, old dead *Pocillopora* colony, reef platform, subtidal, Iles Eparses, Juan de Nova, Juan de Nova Island, Scattered Islands, France, coll. H. Bruggemann, 29 April 2009. — 4 males, 3.4 × 2.2 – 4.2 × 2.7, 1 female, 4.0 × 2.7 (UF 20514*), Stn. EURO-16, -22.34473333° 40.3289°, 15–16 m, dead *Pocillopora verrucosa* head, fore reef, Iles Eparses, Europa, N coast, Europa Island, Scattered Islands, France, coll. M. Guillaume *et al*., 24 April 2009.

Mayotte: 1 male, 5.1 × 3.1 (UF 13611*), MAY08-196, MAY08-St5, 3–4 m, -12.8593° 45.2686°, reef flat, cryptofauna, Pesse en S, Mayotte Island, Comoros Islands, coll. A. Anker & F. Michonneau, 2 June 2008.

Christmas Island: 3 males, 5.2 × 3.0 – 6.6 × 4.0, 2 females, 5.0 × 3.1 – 5.5 × 3.4 (ZRC 2013.1571), Stn. CI03–17, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, early morning, Flying Fish Cove (in coral rocks/rubble; infauna), Christmas Island, 11 February 2012.

Australia: 1 female, 8.45 × 5.30 (UF 17105), AUST-1154, AUST-ST-049, 1-2 m, -14.7429°, 145.5143°, dip net, hand, under rocks and in rubble, reef flat, North Direction Island, S of Lizard Island, Queensland, Australia, coll. A. Anker & R. Lasley, 17 February 2009. — 1 male, 4.8 × 3.1 (UF 16929), AUST-0762, AUST-ST-032, 10–12 m, -14.3902° 145.2737°, hand, high energy fore reef, Washing Machine, Lizard Island, Queensland, Australia, coll., M. Timmers, CReefs Expedition, 13 February 2009. — 1 male (UF 25244), AUST-5548, HI09-042, Heron Island, Queensland, Australia, coll. 17 November 2009. — 1 male (UF 25612), AUST-6063, HI09-090, 4–10 m, algae covered dead *Pocillopora damicornis*, outer reef, exposed, Heron Island, Queensland, Australia, coll. J. Reimer & F. Michonneau, 23 November 2009. — 4 males, 4.2 × 2.7 – 5.3 × 3.3, 5 females, 3.1 × 2.3 – 5.4 × 3.3, 3 ovigerous females, 4.5 × 2.8 – 5.2 × 3.3 (NING 0025), Ningaloo Reef, Western Australia. — 1 male, 5.6 × 3.4 (ZRC 2010.0381*), Ningaloo Reef, Australia. — 1 male, 8.1 × 5.1 (UF 17029), AUST-1036, AUST-ST-041, 2–3 m, hand, dip net, under rocks and in rubble, rubble on sand, corals, back reef flat, 1st snorkel site, Waining Reef, coll. A. Anker & R. Lasley, CReefs Expedition, 15 February 2009. — 1 male, 7.2 × 4.4 (UF 17841), AUST-0923, AUST-ST-043/45, 8–12 m, hand, under rocks and on rubble, lots of rubble, sandy reef bottom/slope, Waining Reef, Queensland, Australia, coll. F. Michonneau & M. Timmers, CReefs Expedition, 15 February 2009. — 1 male, 4.2 × 2.7 (UF 17262*), AUST-1403, AUST-ST-067, 25–30 m, -15.6069° 145.6311, rubble extraction, hand, porous and solid rubble, fore reef, Yonge

Reef, Lizard Island, Australia, coll. S. Smith & K. Mills, CReefs Expedition, 20 February 2009. — 1 female, 4.3 × 2.8 (UF 25553*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009.

Indonesia: 1 male, 4.1 × 2.7 (ZRC 2013.1570*), Stn. BL11-014, BALI-0256, 1–3 m, under rock, sand, scattered coral, rubble, seagrass, Waha, right out front of office, Wanci, Sulawesi, Indonesia, 25 June 2011. — 2 males, 6.0 × 3.8 – 6.3 × 4.0, 3 females, 6.5 × 4.3 – 7.9 × 5.2 (USNM 134520), Poeloe Toekus Island, Indonesia, coll. H. Kellers, November 1925.

Philippines: 1 male, 4.9 × 3.0 (ZRC 2010.0380), B8, Panglao, Philippines. — 1 male, 4.1 × 2.6 (ZRC 2013.1596), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, coll. The Panglao Marine Biodiversity Project, 7 June 2004.

Japan: 1 male, 4.8 × 3.3 (UF 28657*), Stn. FMOK11-St-22, 26.251732° 127.672239°, 0–1 m, in rubble, artificially sheltered fringing reef, Inamuse, Okinawa, Ryukyus, Japan, coll. F. Michonneau & Y. Ryuta, 15 May 2011.

Vanuatu: 1 male, 5.6 × 3.5 (ZRC 2013.1567), Stn. DB01, 15-25 m, 15°33.1'S, 167°17.8'E, coral slope, NE Tutuba Island, Vanuatu, Santo Marine Biodiversity Survey, 10 September 2006. — 1 male, 4.5 × 2.8 (ZRC 2013.1568), Stn. DB80, 18 m, 15°37.1'S, 167°07.5'E, sand and corals on submarine hill, Bruat Channel, Vanuatu, coll. Santo Marine Biodiversity Survey, 02 October 2006. — 1 male, 4.6 × 3.0 (ZRC 2013.1569), Stn. ZB09, 5–7 m, 15°40.6'S, 167°05.1'E, W coast of Malo Island, Vanuatu, Santo Marine Biodiversity Survey, 02 October 2006.

Marshall Islands: 2 males, 5.6 × 3.4 – 6.5 × 4.1 (UF 13733), FM-MAJ08-081, FM-St-MAJ08-07, 0–19 m, 7.1439° 171.2829°, patchy reefs with high coral coverage, cryptofauna, lagoon side, Enecko, Marshall Island, Republic of Marshall Islands, coll. F. Michonneau & S. Kim, 6 April 2008.

Description. Carapace (Pl. 8B) transversely hexagonal, ca. 1.6 times broad as long. Surface convex, glabrous, appearing smooth without magnification, punctate; regions undefined; orbital region slightly raised. Front (Pl. 8C) double-rimmed, bilobed, depressed; lobes convex, joining mesially to form shallow V-shaped notch, margin smooth. Anterolateral margin convex with four distinct teeth, not including external orbital tooth; tooth 1 near and similar in size to outer supraorbital tooth, but broader; tooth 2 broad, anteriorly directed; tooth 3 large, acute, anteriorly directed, tip sharp; tooth 4 small, laterally directed.

Eyestalks minutely granulate. Orbits 0.2 times wide as carapace width, margins smooth; supraorbital margin with median and mediolateral sulci; external orbital margin with small acute tooth superior to small notch; infraorbital margin minutely granulate; inner suborbital tooth projecting anteriorly, rounded, lamelliform. Subhepatic, suborbital, pterygostomial and sub-branchial regions smooth, punctate; epimeral sulcus well defined; pterygostomial region without setae.

Antennules folding transversely. Basal antennal segment rectangular, without lateral flange blocking orbital hiatus, anterolateral angle entering orbital hiatus less than halfway; flagellum free to enter orbital hiatus. Epistome surface smooth. Endostome without longitudinal ridges, divided into four lobes by mesial and lateral fissures.

Third maxilliped quadrate, completely filling the buccal frame, appearing smooth to naked eye, glabrous, punctate. Exopod moderately stout. Endopod ischium sub-rectangular, anterior margin slightly elevated anteriorly 2/3 distance to mesial margin, mesial margin convex, edge setose, lined with sinuous indentions; longitudinal sulcus near mesial margin. Merus subquadrate, with shallow mesial notch; anterior margin sinuous, junction with carpus concave.

Chelipeds (Pl. 8 E, F) unequal, punctate, glabrous. Merus extending beyond lateral margin of carapace more than half its length; anterior, superior surfaces granulate. Carpus smooth, inner angle of dorsal surface produced, forming narrow, rounded tooth. Propodus smooth, minutely punctate. Major chela palm distinctly larger, more swollen than minor chela palm, tip of fixed finger to ventral junction with carpus ca. 2.9 times distance from superior to inferior border; dark pigmentation restricted to fixed finger, cutting edge with one low medial tooth. Fingers dark; tips white, hollowed, spoon-like, with subapical brush of few setae. Dactylus of major chela convex. Dactylus of minor chela relatively straight.

Ambulatory legs (Pl. 8A) long, moderately stout, with long, simple and plumose setae, mostly restricted to extensor margin; extensor surface of merus lined with serrated. Dactyl–propodal locking mechanism well developed, formed by lamellar extension of distal margin of propodus that slides beneath a bulbous flange on dactylus. Tip of dactylus bifid, pigmented spine approximately equal downward-pointing subdistal spine.

Male abdomen (Pl. 8D) long, narrow, with somites 3 to 5 fused, appearing smooth to naked eye, glabrous except few lateral setae on each side of somites 1, 2; somites 1 and 2 smooth; somite 3 not locking with thoracic episternite 7; somite 6 quadrate, approximately broad as long. Telson subtriangular, longer than broad, lateral margins convex, tip rounded, reaching well beyond imaginary line between posterior margin of sternal condyle of first walking leg.

Male thoracic sternum (Pl. 8A) broad, glabrous, appearing smooth to naked eye, minutely granulate, punctate; suture between sternites 1, 2 indicated by few short, simple setae; suture between 3, 4 indicated laterally by short sulci, indicated medially by shallow furrow, almost indiscernible. Press button on sternite 5 closer to suture between sternites 4, 5 than 5, 6. Sternite 7 not divided by transverse sulcus near sternal condyle of third ambulatory leg. Opening for male papilla circular, located on fifth pereopod coxa, covered by lateral lobe of third abdominal segment.

G1 (Pl. 38C) moderately stout; tip subdistally longitudinally hollowed, U-shaped in cross section with margins lined with stout, posteriorly-directed setae; mesial margin of apex expanded as triangular, planar projection.

Diagnosis. Carapace (Pl. 8B) transversely hexagonal, ca. 1.6 broad as long; dorsal surface appearing smooth without magnification, punctate, sometimes granulate laterally; 3M poorly defined; remaining regions poorly or undefined. Front (Pl. 8C) broad; submedian lobes convex, slightly sinuous, or approximately straight, double rimmed, edge minutely granulate or smooth, separated by shallow V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low; tooth 2 broad, large; tooth 3 large, acute, anteriorly directed; tooth 4 small or minute, laterally directed. Anterolateral angle of basal antennal segment not, or slightly, entering orbital hiatus. Pterygostomial region without setae. Chelae (Pl. 8E, F) unequal with tips of fingers hollowed, spoon-like; major chela robust, surface smooth. Ambulatory legs (Pl. 8A) with long, simple and plumose setae; extensor margin of merus serrated or lined with short, distally directed spines; tip of dactylus bifid; distal pigmented spine approximately equal to curved, downward pointing tip. Male thoracic sternum (Pl. 8D) with press button located on sternite 5, slightly closer to suture between sternites 4, 5 than 5, 6. Male abdomen (Pl. 8D) long; somites 3 to 5 fused, sutures indiscernible; somite 6 ca. broad as long; telson longer than broad. G1 (Pl. 38C) moderately stout; tip subdistally longitudinally hollowed, U-shaped in cross section with margins lined with stout, posteriorly-directed setae; apical lobe triangular, planar.

Etymology. The species name refers to the flattened tip of the G1.

Remarks. *Chlorodiella planapexa* sp. nov., is part of the *Chl. laevissima* complex, being externally indistinguishable from *Chl. laevissima* and *Chl. martensi* (see Remarks for *Chl. laevissima* and *Chl. martensi*). These species differ in the apex of the G1. *Chlorodiella planapexa* is distinguished from these two species by possessing a G1 apex that is flattened and triangular (Pl. 38C) [versus elongate, spatulate, and longitudinally hollowed in *Chl. martensi* and spatulate, truncate, and rounded in *Chl. laevissima* (Pls 38D, 39A)]. It is difficult to differentiate between specimens identified as *Chlorodiella laevissima* in historical literature, as all three species in the complex occur sympatrically. However, Dai *et al.* (2008: fig. 170) and Dai & Yang (1991: fig. 170) illustrated the G1 of specimens identified as *Chl. laevissima* which correspond with the *Chl. planapexa* sp. nov., morphology.

Distribution. *Chlorodiella planapexa* is recorded from the Western Indian Ocean to Vanuatu and Okinawa, Japan. It is not known from oceanic Pacific Islands further east (Pl. 46D).

Chlorodiella laevissima (Dana, 1852)

Pls (9, 38D, 47A)

Chlorodius laevissimus Dana 1852a: 80 [Hawaiian Islands]; 1852b: 215 [Hawaiian Islands]; 1855: pl. 12, fig. 4a–g.

Chlorodiella laevissima Rathbun 1906: 857 [Hawaii] (part); 1907: 46 (part) [Rangiroa I.; Papeete, Tahiti; Butaritari I.]. — Forest & Guinot 1961: 95, 96, 101 a–b [Tahiti]. — Serène 1984: 260, fig. 171, pl. XXXVI D (part) [Mauritius].

(?) *Chlorodiella laevissima* Alcock & Anderson 1894: 200 [Palk Strait]. — Alcock 1898: 161 [Andaman Islands, India; Sri Lanka; Mauritius]. — Borradaile 1902: 259 [Maldives and Laccadives]. — Rathbun 1911: 225 [Indian Ocean] (part). — Nobili 1907: 393 [List] [Rikitea and Mangareva, French Polynesia]. — Edmondson 1933: 251, fig. 152f [Review]; 1962: 281, fig. 23e [Hawaii]. — Miyake 1936: 508 [Yaeyama, Japan]. — Balss 1938a: 53 [Apamama, Aranuka, and Tamana, Gilbert Islands; Niue, Ellice Island; Jaluit and Likieb, Marshall Islands; Viti Levu and Namuka, Fiji Island]. — Lin 1949: 23 [Taiwan]. — Tweedie 1950b: 120 [Cocos Keeling Islands]. — Holthuis 1953: 15 [Saipan; Onotoa, Gilbert Islands]. — Sankarankutty 1962: 136, figs. 32-33 [Niell Island, Car Nicobar]. — Guinot 1962a: 9 [Gilbert Islands]; 1964: 70 [Aldabra]; 1967c: 262 [list]. — Miyake & Takeda 1968: 393 [Key]. — Seréne 1968: 81 [SE Asia]. — Ooishi 1970: 93 [Ogasawara, Japan]. — Kensley 1970: 107, fig. 3 a-d [Mozambique]; 1981: 44 [Mozambique]. — Seréne et al. 1976: 18 [Ambon I., Indonesia]. — Takeda 1977: 85 [Mage Jima I., Japan]; 1989: 159 [Oshima Passage, Japan]. — Chen & Lan 1978: 268, figs. 2, 7 (12, 13), pl. 1, fig. 2 [Xisha Islands]. — Ribes 1978 [Reunion I.]. — Thomassin 1978 [Tulear, Madagascar]. — Titgen 1987: 107, figs. 1e-h [Hawaii]. — Peyrot-Clausade 1989: 112 [Tikehau, Tuamotu]. — DeFelice *et al*. 1998: 16 [Midway Atoll, Hawaiian Is.]. — Coles *et al*. 2001: 54 [List]. — DeFelice *et al.* 2002: 30, 72 [French Frigate Shoals, Hawaiian Is.]. — Coles *et al* 2002a: 269, 333 [Oahu]. — Davie 2002: 519 [List]. — Godwin & Bolick

2006: 39, 49 [Honolulu, Hawaiian Is.]. — Coles *et al.* 2008: 62 [List]. — Coles & Swensen 2010: 87 [List].

Chlorodiella niger, Edmondson 1925: 44 [Hawaiian Islands] (part). [not *Chlorodiella nigra* (Forskål 1775)]

Chlorodiella nigra, Rathbun 1906: 857 [Hawaiian Islands] (part). [not *Chlorodiella nigra* (Forskål 1775)]

Material examined. *Scattered Islands:* 1 male (damaged) (UF 21089A*), Stn. GLOR-17, -11.57141667° 47.28428333°, 8 m, dead *Pocillopora eydouxi* head, reef front, Iles Eparses, Glorieuses, Glorieuses Island, Scattered Islands, France, coll., 8 May 2009. — 1 male, 5.5 × 3.6 (UF 21117*), Stn. GLOR-17, -11.57141667° 47.28428333°, 8 m, dead *Pocillopora eydouxi* head, reef front, Iles Eparses, Glorieuses, Glorieuses Island, Scattered Islands, France, coll. 8 May 2009. — 1 male, 5.1 × 3.4 (UF 20739*), Stn. JDNO-17, -17.07466667° 42.76605°, 5 m, old dead *Pocillopora*, fore reef slope, Iles Eparses, Juan de Nova, Juan de Nova Island, Scattered Islands, France, coll. H. Bruggemann, 29 April 2009. — 1 male, 4.5 × 2.8 (UF 20556), Stn. EURO-18, -22.34471667° 40.33305°, 0 m, in *Pocillopora* head, partially dead, reef flat, Iles Eparses, Europa, N coast, Europa Island, Scattered Islands, France, coll. M. Malay, 24 April 2009.

Reunion Island: 2 male, 3.6 × 2.2 – 5.4 × 3.2, 1 female, 3.3 × 2.0, 1 ovigerous female, 5.9 × 3.5 (UF 13055*), SWIO-17, 8–9 m, -21.1936° 55.2824°, Maison Verte/Cimetiere, Saint-Leu, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al.*, 13 August 2007. — 1 female (damaged) (UF 13094*), SWIO-26, 6-15 m, -21.1533° 55.2811°, Sec Jaune, Saint-Leu, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al.*, 17 August 2007. — 1 ovigerous female, 6.0 × 3.7 (UF 12675*), BREU-0474, SWIO-10, 8 m, -21.1116° 55.249°, cryptofauna search, from reef matrix (old dead digitate *Acropora* head), fore reef, Souris Chaude, Trois-Bassins, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann, *et al*., 9 August 2007. — 3 males, 3.3 × 2.0 – 6.5 × 4.0 (UF 13085*), SWIO-10, 8 m, -21.1116° 55.249°, Souris Chaude, Trois-Bassins, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann, *et al*., 9 August 2007.

Chagos: 1 male, 4.3 × 2.1 (ZRC 2013.0771), CH0107, 10m approx., dead branching coral heads, outer reef, Salomon, Chagos Archipelago, coll. C. Head & H. Koldeway, 18 February 2013. — 1 male, 3.6 × 2.9, 1 female, 1 ovigerous female (ZRC 2013.0776), CH0260, 10m approx., dead branching coral heads, outer reef, Salomon Chagos Archipelago, coll. C. Head & H. Koldeway, 20 February 2013.

Australia: 1 male, 3.9 × 2.5 (UF 24870*), Stn. HI09-011, -23.47221667° 151.9504667°, 9–10 m, in rubble, reef slope, coral cover, rubble patches, Heron Island, Pinacle, Queensland, Australia, coll. S. McKeon, 13 November 2009. — 1 female, 7.2 × 4.6 (UF 24810*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 female, 6.7 × 4.4 (UF 24804*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009.

Japan: 1 female, 5.3 × 3.5 (UF 28664*), Stn. FMOK11-St-22, 26.251732° 127.672239°, 0–1 m, in rubble, artificially sheltered fringing reef, Inamuse, Okinawa, Ryukyus, Japan, coll. F. Michonneau & Y. Ryuta, 15 May 2011.

Mariana Islands: 2 males, 4.6 × 2.8 – 4.7 × 3.0, 3 ovigerous females, 4.7 × 2.9 – 5.3 × 3.2 (USNM 94024), Loc-D6, lagoon W of Saipan, Mariana Islands, coll. P. Cloud, Geological Survey, 6 May 1949.

Caroline Islands: 1 male, 4.6 × 2.9, 2 females, 4.2 × 2.6 – 6.3 × 3.8 (USNM 106676), Stn. 372, outer reef flat, seaward reef, Ifaluk Atoll, N end of Falarik, coll. Atoll Survey Team, Pacific Science Board, 22 September 1953. — 1 male, 4.3 × 2.6 (USNM 1191865), Ifaluk Atoll, Caroline Islands, coll. B. Abbott, Acc. 200652. — 1 male, 3.7 × 2.2 (USNM 1191855), Acc. 200652, Ifaluk Atoll, Caroline Islands, coll. B. Abbott.

Marshall Islands: 1 male, 4.3 × 2.8 (USNM 1191737), Acc. 176603, lagoon reef, Latoback Island, Rongerik, coll. F. Bayer & F. Zimmerman, 20 August 1947. — 1 male, 5.9 × 3.7 (USNM 1191736), Acc. 176603, lagoon reef, Latoback Island, Rongerik, coll. F. Bayer & F. Zimmerman, 20 August 1947. — 1 male, 5.4 × 3.3 (USNM 1191731), Acc. 176603, lagoon reef, Latoback Island, Rongerik, coll. F. Bayer & F. Zimmerman, 20 August 1947. — 1 male, 5.6 × 3.4 (USNM 1191742), Acc. No. 176 603, 192(3), Bikini Island, Bikini Atoll, 16 August 1947, FMB. — 1 male, 3.9 × 2.3 (USNM 266915), *Halemeda*, ocean side, Igurin Island, Marshall Islands, coll. D. Reish, Eniwetok Marine Biological Laboratory Reference Collection, 27 August 1956, acc. 477423.

Kiribati: 1 male, 6.2 × 4.0, 1 female, 5.4 × 3.4 (UF 10563*), BPALM-943, PALB4-DP, 35 ft, 5.8958° -162.0815°, from dead *Pocillopora ?verrucosa* head, outer reef slope, N side of Atoll, Palmyra Atoll, Line Islands, USA, coll. G. Paulay & N. Knowlton, 19 August 2005. — 1 juvenile (UF 11174*), MSR-154-DP, KINF16-DP, 40 ft, 6.3796° -162.3648°, dead *Pocillora ?verrucosa* head, S shore of atoll, Kingman Reef, Line Islands, USA, coll. 28 August 2005. — 1 male, 4.7 × 3.0 (UF 11646*), BTAB-035, GP-Loc-843, 10-23 m, 3.8051° -159.3021°, under rocks, outer reef slope, SSW side of atoll, Tabuaeran Atoll, Line Islands, Kiribati, coll., G. Paulay, 13 August 2005. — 1 male, 8.7 × 5.3 (UF 13803*), BPAL-1100, PALB10-DP, 0–16.2 m, 5.8663° -162.0581°, in dead *Pocillopora* head, outer reef slope, S side of atoll, Palmyra

Atoll, Line Islands, USA, coll. M. Malay, 22 August 2005. — 5 males, 2.9 × 1.8 – 5.4 × 3.4, 2 females, 3.0 × 1.8 – 3.8 × 2.4, 3 ovigerous females, 4.1 × 2.6 – 6.1 × 3.7 (UF 11071*), BTAB-586, GP-Loc-843-DP, 10–23 m, 3.8051° -159.3021°, quantitative sample from one dead *Pocillopora ?ver*, outer reef slope, SSW side of atoll, Tabuaeran Atoll, Line Islands, Kiribati, coll. N. Knowlton & G. Paulay, 13 August 2005. — 1 juvenile (UF 11179*), MSR-159-DP, KINF16-DP, 40 ft, 6.3796° -162.3648°, dead *Pocillopora verrucosa?* head, outer reef slope, S shore of atoll, Kingman Reef, Line Islands, USA, coll. 28 August 2005. — 1 male, 5.8 × 3.4, 1 female, 6.0 × 3.8 (UF 10562*), BTAB-632, GP-Loc-843-H, 10-23 m, 3.8051° -159.3021°, from *Halimeda* sample, outer reef slope, SSW side of atoll, Tabuaeran Atoll, Line Islands, Kiribati, coll. G. Paulay & N. Knowlton, 13 August 2005. — 1 ovigerous female, 6.6 × 4.0 (UF 10566*), MSR-156, KINF16-DP, 10–15 m, 6.3796° -162.3648°, from dead *Pocillopora ?verrucosa*, outer reef slope, S shore of atoll, Kingman Reef, Line Islands, USA, coll. M. Malay, 28 August 2005. — 1 ovigerous female, 5.6 × 3.5 (UF 11070*), BTAB-585, GP-Loc-843-DP, 10-23 m, 3.8051° -159.3021°, quantitative sample from one dead *Pocillopora ?ver*, outer reef slope, SSW side of atoll, Tabuaeran Atoll, Line Islands, Kiribati, coll. N. Knowlton & G. Paulay, 13 August 2005. — 2 males, 4.1 × 2.6 – 5.8 × 3.6, 1 female, 4.7 × 3.0 (USNM 94025), G.O.C.-51, 8–15 ft, from thickly set coral masses, about 3 1/4, mi. N 31° W, from Tabuarorae Maneaba near the center of Te Rawa ni Bao, a pass in the S part of the leeward reef, Onotoa, Gilbert Islands, coll. P. Cloud, Geol. Survey, 23 August 1951.

Hawaiian Islands: 2 males (larger = 7.90 x 5.43), 1 female, 1 ovigerous female (AMNH 9619), Midway Island, February – March, 1941, coll. Phil Spicer. From W. J. Clench. — 1 male, 7.9 × 5.1 (ZRC 2008.0554), Kewalo Beach, Oahu, Hawaii, coll. 22 January 2000, det. P. Ng. — 2 males, 7.9 × 4.9 – 9.2 × 5.9, 1 ovigerous female, 7.2 × 4.5 (ZRC 2013.1566), surf zone, on sea wall, Kewalo, Ala Moana area, Waikiki, Oahu, Hawaii, coll. P. Ng & S. Tan, 22 January 2000. — 1 male, 7.5 × 4.6, 1 ovigerous female, 5.3 × 3.1 (UF 17927*), ZZZ-073307, in/on *Pocillopora damicornis*, Kaneohe Bay, Oahu Island, Hawaiian Islands, USA, coll. S. McKeon, July 2008. — 1 male, 3.7 × 2.3 (UF 12363), FFS-0086, 4 feet, 23.8732° -166.2348°, dive, rubble brush, reef crest, French Frigate Shoals, Hawaiian Islands, USA, coll. B. Zgliczynski *et al.*, 16 October 2006. — 1 male, 6.1 × 3.8 (UF 12007), BFFS-53, FFS-OAHU-RUBEX, rubble extraction, Oahu, Hawaiian Islands, USA, October 2006. — 1 male, 6.4 × 3.8 (UF 12328*), BFFS-1238, FFS-0091, 15 ft, 23.8733° -166.2347°, back reef, French Frigate Shoals, Hawaiian Islands, USA, coll. R. Brainard & B. Zgliczynski, 16 October 2006. — 4 males, 7.7 × 4.8 – 9.0 × 5.7, 1 ovigerous female, 7.7 × 4.7 (USNM 48957), reef, low tide, Pukoo, Molakai, Hawaiian Islands, coll. College of Hawaii, Acc. 58008. — 5 males, 5.0 × 3.1 – 9.0 × 5.5, 8 females, 5.1 × 3.1 – 7.8 × 4.8, 4 ovigerous females, 4.7 × 2.9 – 7.3 × 4.5, 1 juvenile (USNM 49036), Acc. 57062, the reef between Waikiki Beach and Honolulu Harbor, Oahu, coll. J. Bridwell. — 2 males, 5.6 × 3.5 – 6.6 × 4.0, 3 females, 5.0 × 3.1 – 6.2 × 3.7, 1 ovigerous female, 5.9 × 3.5 (USNM 25357), Waikiki Beach, Hawaiian Islands, coll. US Fish Commission. — 1 male, 4.5 × 2.8, 1 female, 4.7 × 2.9 (USNM 29445), French Frigate Shoals, coll. Str. Albatross. — 11 males, 4.6 × 2.9 – 8.1 × 5.3, 22 females, 4.0 × 2.6 – 8.1 × 5.1, 2 ovigerous females, 5.5 × 3.3 – 6.5 × 4.1 (USNM 29451), Laysan, Hawaiian Is., coll. US Fish Commission, Steamer Albatross, May 1902.

Society Islands: 1 male, 5.0 × 3.1 (UF 9632*), MMOOR-29.14, MMOOR-29, 15–22 m, -17.506° -149.759°, outer slope, ENE shore of Moorea, Temae, Moorea Island, Society Islands, French Polynesia, coll. M. Malay & E. Emmanuelli, 27 May 2006. — 1 male, 5.5 × 3.4 (UF 9851*), BMOO-1190, GP-Loc-878, 0–2 m, -17.4982° -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 ovigerous female, 5.4 × 3.4 (UF 9838*), BMOO-1192, GP-Loc-878, 0–2 m, -17.4982° -149.8636°, by hand, within reef rock rubble, fringing and patch reef at mouth of bay, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 male, 6.0 × 3.7 (USNM 1191714), Acc. No. 213 821, 62–57, W of Motu Tapee, Bora Bora, coll. 25 April 1957. — 4 males, 4.7 × 2.9 – 7.2 × 4.4, 3 females, 3.9 × 2.4 – 5.1 × 3.1, 3 ovigerous females, 5.7 × 3.5 – 6.1 × 3.8, 2 juveniles (USNM 1191713), Acc. No. 213 821, 42–57, NW of Motu Uta Island, Papeete Harbor, Tahiti, coll. 20 April 1957. — 1 male, 5.5 × 3.4 – 6.1 × 3.8, 1 ovigerous female, 5.3 × 3.3 (USNM 1191745), Acc. No. 213 821, Sta. 80-57, 2–3 ft, branching coral, off N end Tauru Island, Raiatea Islands, Leeward Islands, Society Islands, French Polynesia, South Pacific Ocean, coll. W. Schmitt, 29 April 1957.

Tuamotu Islands: 1 male, 4.1 × 3.1 (USNM 1191739), fringing reef, sea beach, Fakarava, Paumotus, coll. US Fish Commission Steamer Albatross, 13 October 1899.

Diagnosis. Carapace (Pl. 9B) transversely hexagonal, ca. 1.6 broad as long; dorsal surface appearing smooth without magnification, punctate, sometimes granulate laterally; 3M poorly defined; remaining regions undefined. Front (Pl. 9C) broad; submedian lobes convex, slightly sinuous, or approximately straight, double rimmed, edge minutely granulate or smooth, separated by shallow V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low; tooth 2 broad large; tooth 3 large, acute, anteriorly directed; tooth 4 small or minute, laterally directed. Anterolateral angle of basal antennal segment not or slightly projecting into orbital hiatus. Pterygostomial region without setae. Chelae (Pl. 9E, F) unequal with tips of fingers hollowed, spoon-like; major chela robust, surface smooth. Ambulatory legs (Pl. 9A) with long, simple and plumose setae; extensor margin of merus serrated or lined with short, distally directed spines; tip of dactylus bifid; length of distal pigmented spine approximately equal to curved, downward pointing tip. Male thoracic sternum (Pl. 9D) with press button located on sternite 5, slightly closer to suture between sternites 4, 5 than 5, 6. Male abdomen (Pl. 9D) long; somites 3 to 5 fused, sutures indiscernible; somite 6 ca. broad as long; telson longer than broad. G1 (Pl. 38D) with subdistal spines and several long, stout, posteriorly-directed, curved setae; apex spatulate, truncate, distal margin rounded.

Remarks. *Chlorodiella laevissima* has been historically confused with *Chl. cytherea.* Both species have very similar carapace dimensions, anterolateral teeth, chelae, and ambulatory legs. Based on molecular data, The easiest character used to distinguish between the two species is the shape of the G1 apex. *Chlorodiella laevissima* complex species (*Chl. laevissima*, *Chl. martensi*, and *Chl. planapexa*) have G1 apexes that are spatulate or triangular (Pls 38C, D, 39A), whereas *Chl. cytherea* has a G1 apex that is “curled” or “hooked” (Pls 37C, D, 38A, B). These species can also be distinguished by the lateral regions of the carapace and setation of the pterygostomial region. *Chlorodiella laevissima* complex species have lateral regions of the carapace that are not indicated (Pls 8–10) and pterygostomial regions without setae [versus elevated lateral regions (Pls 3–7) and a pterygostomial regions with plumose setae diagonally from posterior to lateral surface in *Chl. cytherea*]. However, some specimens of *Chl. cytherea* have lateral regions that are not elevated, especially small specimens, and the setation of the pterygostomial region can wear away with age or abrasion.

Chlorodiella laevissima is differentiated from *Chl. martensi* and *Chl. planapexa* in having a relatively truncate, spatulate G1 apex with a rounded distal margin (Pl. 38D) [versus spatulate, elongate, distally pointed in *Chl. martensi* and planar and triangular in *Chl. planapexa* (Pls 38C, 39A)].

Distribution. *Chlorodiella laevissima* is known from the Hawaiian Islands and French Polynesia to the Western Indian Ocean (Pl. 47A).

Chlorodiella martensi (Krauss, 1843)

Pls (10, 39A, 47B)

Menippe martensi Krauss 1843: 34, pl. 2, fig. 1 [South Africa].

Chlorodiella martensi Serène 1968: 81 [List].

Chlorodiella laevissima, Rathbun 1906: 857 [Hawaiian Islands] (part); 1907: 46 (part) [Fakarava I.] 1911: 225 [Seychelles] (part). — ?Sakai 1935: 165, fig. 81, pl. 43 fig. 3 [Japan]; 1939, p. 508, fig. 44, pl. 62, (3) [Simoda, Japan]; 1965, p. 151, pl. 75, fig. 1 [Sagami Bay, Japan]; 1976: 465, fig. 250 [Japan]. — ?Tweedie 1950b: 120 [Cocos Keeling Islands]. — ?Ooishi 1970: 93 [Ogasawara, Japan]. — Serène 1984: 260–261, fig. 172 pl. XXXVI E (part) [Key, Diagnosis] [Mauritius]. — ?Peyrot-Clausade 1989: 112 [Tikehau, Tuamotu]. — ?Takeda 1977: 85 [Mage Jima I., Japan]. [not *Chlorodiella laevissima* (Dana, 1852)]

Material examined. *Reunion Island:* 1 male, 8.0 × 5.0 (UF 12861*), BREU-1326, SWIO-23, 10–19 m, -21.1555° 55.2811, dive, under rocks, rocky slope/ basalt blocks/ fore reef, Sec Jaune, Saint-Leu, Reunion Island, Mascarene Islands, coll. H. Bruggemann, *et al*., 17 August 2007.

Amirante Islands: 8 males, 7.4 × 5.1 – 10.1 × 6.6, 8 females, 7.2 × 5.1 – 8.5 × 5.5, 3 ovigerous females, 8.5 × 5.5 – 8.9 × 5.6 (dry) (USNM 41253), Stn. E-21, 30 fms., Amirante, coll. H.M.S. Sealark, 17 October 1905.

Christmas Island: 2 males, 4.6 × 2.9 – 8.3 × 5.1, 1 female, 6.5 × 4.3 (ZRC 2013.1574), Stn. CI03–17, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, early morning, Flying Fish Cove (in coral rocks/rubble; infauna), Christmas Island, 11 February 2012.

Indonesia: 1 female, 6.3 × 4.1 (ZRC 2013.1572*) Stn. BL11-013, BALI–0375, 22–24 m, rubble extractions, reef wall/slope, Sambu, Wanci, Sulawesi, Indonesia, coll. 23 June 2011. — 2 males, 5.3 × 3.3 – 6.3 × 3.8, 3 females 5.0 × 3.1 (ZRC 2013.1573) Stn. BL11-007, BALI-0303, 5–15 m, rubble extraction, coral reef, steep slope/wall, Sambu, Wanci, Sulawesi, Indonesia, coll. 23 June 2011.

Philippines: 1 male, 7.4 × 4.8 (USNM 15274), Stn. 5325, Hermanos Island, off N. Luzon, Philippine Islands, coll. Philippine Expedition 1907–1910, Albatross, 12 November 1908.

Australia: 2 males, 3.9 × 2.4 – 6.0 × 4.0, 2 ovigerous females, 3.8 × 2.5 – 3.9 × 2.5, 3 juveniles, 2.6 × 1.6 – 3.1 × 2.0 (ZRC 2010.0382) NING 0179, Ningaloo Reef, Australia. — 1 male, 6.1 × 4.1 (UF 17836*), AUST-0809, AUST-ST-000, 10–12 m, rubble, Lizard Island, Queensland, Australia, coll. 13 February 2009. — 1 male, 6.3 × 4.2 (UF 24655*), AUST-4581, HI09-001, 1–4 m, -23.452° 151.8671°, by hand, in rubble, lagoonal patch reefs, Wistari Reef, Heron Island, Queensland, Australia, coll. R. Lasley, 11 November 2009. — 1 female, 4.6 × 3.3 (UF 24745*), Stn. HI09-007, -23.4321333° 151.93375°, in rubble, back reef, Heron Island, First Point, North Heron Reef, Queensland, Australia, coll., 12 November 2009. — 1 female (damaged), (UF 25519*), Stn. HI09-076, -23.4331667° 151.91708333°, 6–16 m, in rubble, outer reef, Heron Island, North Heron, Queensland, Australia, coll., 22 November 2009. — 1 male, 11.4 × 7.4 (UF 24995*), Stn. HI09-024, -23.26788333° 151.9502667°, 18–21 m, back reef, Heron Island, Broomfield

Reef, Queensland, Australia, coll. S. McKeon & F. Michonneau, 15 November 2009. — 1 male, 5.7 × 3.9 (UF 24916*), Stn. HI09-019, -23.43135° 152.03375°, 1–2 m, under rock, reef crest, reef flat, Heron Island, Sykes Reef, Queensland, Australia, coll. F. Michonneau & R. Lasley, 14 November 2009. — 1 female, 6.1 × 3.9 (UF 21545*), Stn. NIN09-St-10, -22.68118° 113.6015°, 24–28 m, in rubble, Ningaloo Reef, N outside of reef, Western Australia, Australia, coll. L. Avery & M. Capa, 16 May 2009.

Japan: 1 male (damaged) (UF 7176*), BOKI-26-CC, GP-Loc-799, 18-22 m, 26.7392° 127.8101°, under rocks, outer reef slope, NW end of island, Kanan-zaki, Ie Island, Okinawa, Japan, coll. G. Paulay & Kinjo, 8 July 2004.

Mariana Islands: 1 male, 4.6 × 2.9, 1 ovigerous female, 5.1 × 3.1 (UF 3136), LAK-127, 28 m, 13.5369° 144.8016°, in rubble, close to Gun Beach, Dos Amantes, Guam Island, Mariana Islands, USA, coll. L. Kirkendale, 21 June 2002. — 2 males, 5.7 × 3.6 – 6.0 × 3.8, 3 females, 4.5 × 2.8 – 5.0 × 3.2, 2 juveniles, 3.1 × 2.0 – 3.3 × 2.0 (USNM 1188318), 9 m, 300 ns north of boat basin, reef front, Agana Bay, Guam, coll. J. Dominguez, 23 October 1984. — 2 males, 4.2 × 2.2 – 5.3 × 3.4 (USNM 1184677), 8–9 m, reef front, off Alupat Island, Agana Bay, Guam, coll. R. Kropp & J. Dominguez, 3 February 1984. — 1 male, 5.6 × 3.6, 1 female, 4.9 × 3.2 (f/ UF 1256*), ZZZ-085731, 10–20 feet, among rocks, near harbor entrance, glass breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 22 August 1984.

Caroline Islands: 1 male, 5.8 × 3.6, 1 female, 5.6 × 3.5, 1 ovigerous female, 6.6 × 4.2 (USNM 1191740), Sta. 137, 230 087, Polim Reef, Kapingamarangi, coll. 12 August 1954, GVF. — 1 male, 4.8 × 3.1 (USNM 128133), Woleai Atoll, in lagoon opposite, Utagal Island, Caroline Islands, coll. L. McLoskey & H. Roberts, 28 July 1968.

New Caledonia: (?) 1 female, 7.1 × 4.8 (UF 37971*), NewC13-LOF35, -18.8774° 163.44°, backreef, barrier, leeward side, Cook Reef, New

Caledonia, coll. N. Evans, 9 November 2013, Global Reef Expedition, M/Y Golden Shadow. — (?)1 male, 4.5 × 3.3 (UF 37969*), NewC13-718, NEST30, 0–3 m, -18.4879° 163.096°, reef crest, fore reef, back reef, shoreline, dense, Surprise island, New Caledonia, coll. N. Evans, 20 November 2013.

Vanuatu: 2 males, 4.9 × 3.2 – 7.6 × 4.9, 1 damaged male (ZRC 2013.1575), Stn. ZB 6, 30 m, 15°36.8'S, 167°01.3'E, patches of sand, SW Urélapa Island, Vanuatu, coll. Santo Marine Biodiversity Survey 28 September 2006. — 1 male, 6.2 × 4.1, 1 female, 4.1 × 2.5 (ZRC 2013.1576), Stn. DB 29, 15 m, 15°38.9'S, 167°05.1'E, sand around coral patches, W Malo Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 17 September 2006. — 1 male, 7.7 × 4.9 (ZRC 2013.1577), Stn. DB01, 15–25 m, 15°33.1'S, 167°17.8'E, coral slope, NE Tutuba Island, Vanuatus, Santo Marine Biodiversity Survey, 10 September 2006. — 2 males, 4.3 × 2.9 – 6.1 × 4.0, 2 females, 4.2 × 2.9 – 6.0 × 3.9 (ZRC 2013.1578), Stn. DB63, 21 m, 15°26.9'S, 167°15.8'E, sand, dead and live corals, SE Aésé Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 25 September 2006. — 2 males, 4.9 × 3.2 – 7.6 × 4.9, 1 damaged male (ZRC 2013.1575), Stn. ZB 6, 30 m, 15°36.8'S, 167°01.3'E, patches of sand, SW Urélapa Island, Vanuatu, coll. Santo Marine Biodiversity Survey 28 September 2006.

Niue Island: 1 male, 6.7 × 4.0 (UF 2492), BNIUE-403, 10–15 m, undersides of rocks, outer reef slope, just N of boat landing, Avatele, Niue Island, coll. B. Holthuis & G. Paulay, 25 October 1991.

Line Islands: 1 male, 10.4 × 6.6 (UF 11190*), MSR-237-DP, Clam Gardens-001, 13.5 m, 6.3908° -162.3419°, dead *Pocillopora verrucosa*? head, W or channel buoy of La Paloma Pass lagoon, Kingman Reef, Line Islands, coll. 26 August 2005. — 1 male, 6.9 × 4.3 (UF 11648*), BTAB-021, GP-Loc-842, 10–20 m, 3.8511° -159.3646°, under dead rubble (dead *Acropora* slabs), outer reef slope, just south of main reef pass, W side, Tabuaeran Atoll, Line Islands, Kiribati, coll. G. Paulay, 12 August 2005. — 1 male, 4.8 × 3.0, 1 female, 6.1 × 3.9 (UF 11107*), BPALM-886, GP-Loc-848-H, 9–15 m, 5.8693° -162.0757°, from *Halimeda*, outer reef slope, SSW side of atoll, Palmyra Atoll, Line Islands, USA, coll. N. Knowlton & G. Paulay, 18 August 2005. — 1 male, 9.8 × 6.1, 1 female, 9.2 × 5.6 (UF 11066*), BTAB-521, GP-Loc-841-DP, 10-15 m, 3.8418° -159.3608°, dead *Pocillopora verrucosa*? head, outer reef slope, S of main reef pass, W side, Tabuaeran Atoll, Line Islands, Kiribati, coll. N. Knowlton & G. Paulay, 12 August 2005.

Hawaiian Islands: 3 males, 6.8 × 4.5 – 7.8 × 5.0, 2 females, 6.1 × 4.0 – 6.3 × 4.2 (USNM 29442), Stn. 3876, Auau Channel, Hawaiian Islands, coll. U.S. Fish Commission, Streamer Albatross. — 2 males, 6.5 × 4.3 – 8.7 × 5.5 (USNM 29436), Stn. 3848, Molokai Island, Hawaiian Islands, coll. U.S. Fish Commission, Steamer Albatross. — 2 males, 6.1 × 4.0 – 7.5 × 5.0 (USNM 76223), Stn. 3876, 13 to 43 fathoms, Auau Channel, Hawaii, coll. US Fish Commission Steamer Albatross. — 3 males, 5.6 × 3.8 – 9.3 × 6.0 (USNM 29438), Stn. 3871, 13 to 43 fathoms, Auau Channel, Hawaii, coll. US Fish Commission Steamer Albatross. — 3 males, 6.1 × 4.0 – 9.1 × 6.0, 1 female, 4.3 × 2.9 (USNM 29441), Stn. 3874, 13 to 43 fathoms, Auau Channel, Hawaii, coll. US Fish Commission Steamer Albatross. — 1 male, 5.0 × 3.4 (USNM 29446), Stn. 4034, 28 to 14 fathoms, Penguin Bank, Hawaiian Islands, coll. US Fish Commission, Steamer Albatross. — 3 males, 5.4 × 3.6 – 7.9 × 5.0 (USNM 29447), Stn. 4061, 24 to 83 fathoms, NE coast of Hawaii, coll. US Fish Commission, Steamer Albatross. — 5 males, 5.5 × 3.8 – 9.3 × 6.1, 4 females, 4.9 × 3.3 – 7.1 × 4.6, 2 ovigerous females, 5.7 × 3.8 – 6.8 × 4.4 (USNM 29435), Stn. 3847, 23 to 73 fathoms, S coast of Molokai, Waikiki Beach, Honolulu, coll. US Fish Commission, Steamer Albatross. — 1 male, 6.7 × 4.4, 2 ovigerous females, 8.0 × 5.1 – 7.9 × 5.0 (USNM 29437), Stn.

3849, 23 to 73 fathoms, S coast of Molokai, Waikiki Beach, Honolulu, coll. US Fish Commission, Steamer Albatross.

Society Islands: 1 female, 5.0 × 3.3 (UF 10065*), BMOO-1849, GP-Loc-895, 35–37 m, -17.4803° -149.8539°, by hand, extracted from inside rubble, outer reef slope, fore reef of NE of Tareu Pass, Moorea, Society Islands, French Polynesia, coll. C. McKeon *et al.*, 2 August 2006. — 1 female, 5.3 × 3.3 (UF 10066*), BMOO-1850, GP-Loc-895, 35–37 m, -17.4803° -149.8539°, by hand, extracted from inside rubble, outer reef slope, fore reef of NE of Tareu Pass, Moorea, Society Islands, French Polynesia, coll. C. McKeon, *et al.*, 2 August 2006. — 1 male, 9.0 × 5.9 (UF 9966*), 10–15 m, -17.4756° -149.8344°, by hand, partly in sand, under rocks, outer reef slope, fore reef between Cook's and Opunohu bays, Moorea, coll. C. McKeon *et al.*, 19 July 2006. — 1 male, 7.6 × 4.7 (UF 9633*), MMOOR-29.13, MMOOR-29, 15-22 m, -17.506° -149.759°, 2 dives, outer slope, ENE shore of Moorea, Temae, Moorea Islands, Society Islands, French Polynesia, coll. M. Malay & E. Emmanuelli, 27 May 2006. — 1 male (damaged) (UF 9626*), MMOOR-26.4, MMOOR-26, 12–22 m, -17.5333° -149.8333°, outer slope, W coast of Moorea, Moorea Island, Society Islands, French Polynesia, coll. M. Malay, 24 May 2006. — 1 female, 6.9 × 4.4 (UF 9759*), BMOO-1569, GP-Loc-886, 22 m, -17.4836° -149.8581°, by hand, extracted from *Pocillopora* rubble, outer reef slope, fore reef NE of Tareu Pass, Moorea Island, Society Islands, French Polynesia, coll. C. McKeon *et al.*, 24 July 2006.

Gambier Islands: 1 male, 6.7 × 4.3 (UF 35471), Stn. GAMG-56, -23.0776° -134.88840039°, 22.48 m, in rubble, windward fore reef, Totegegie Airport, Gambier Islands, French Polynesia, coll. J. Moore, 6 February 2013.

Tuamotu Islands: 1 male, 5.0 × 3.3 (UF 35392), Stn. GAMV-28, -21.4445° -136.4037°, 31.77 m, leeward fore reef, Maturei Vavao Atoll, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 26 January 2013. —

1 male, 6.5 × 4.1 (UF 35391), Stn. GAMV-28, -21.4445° -136.4037°, 31.77 m, leeward fore reef, Maturei Vavao Atoll, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 26 January 2013. — 1 male, 7.5 × 4.7, 1 female, 7.0 × 4.3 (UF 1627*), BRNG-009, Rangiroa Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 10 October 2001. — 1 male, 4.6 × 2.7 (UF 9637*), MFAKA-07.16, MFAKA-07, 5–18 m, -16.0833° -145.7167°, 2 dives, outer slope, closer to lighthouse, SE of Mfaka-6, E of the N pass of Fakarava Atoll, Fakarava Atoll, Tuamotu Islands, French Polynesia, coll. M. Malay, 9 June 2006.

Marquesas: 1 male, 6.6 × 4.2 (UF 30027*), Stn. MQ012, -8.80868333° -140.04908333°, 14 m, fine sand plain, slope of large coral blocks, SW of Haataivea Bay, Nuku Hiva, Marquesas Islands, French Polynesia, coll. N. Evans, *et al.*, 27 November 2012. — 1 male, 4.7 × 3.3 (UF 30014), Stn. MQ010, -7.95515° -140.66171667°, 24 m, alternating buttresses separated by zones of block, Charner Bay, N side of island, Eiao, Marquesas Islands, French Polynesia, coll. N. Evans, *et al.*, 26 November 2012.

Diagnosis. Carapace (Pl. 10B) transversely hexagonal, ca. 1.6 broad as long; dorsal surface appearing smooth without magnification, punctate; 3M poorly; remaining regions undefined. Front (Pl. 10C) broad; submedian lobes convex or approximately straight, double rimmed, edge minutely granulate or smooth, separated by shallow V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low; tooth 2 broad, large; tooth 3 large, acute, anteriorly directed; tooth 4 small or minute, laterally directed. Anterolateral angle of basal antennal segment slightly or not projecting into orbital hiatus. Pterygostomial region without setae. Chelae unequal with tips of fingers hollowed, spoon-like; major chela robust, surface smooth. Ambulatory legs (Pl. 10A) with long, simple and plumose setae; extensor margin of merus serrated or lined with short, distally directed spines;

tip of dactylus bifid; distal pigmented spine approximately equal to curved, downward pointing tip. Male thoracic sternum (Pl. 10D) with press button located on sternite 5, slightly closer to suture between sternites 4, 5 than 5, 6. Male abdomen (Pl. 10D) long; somites 3 to 5 fused; somite 6 ca. broad as long; telson longer than broad. G1 (Pl. 39A) tip elongate, spade-like, concave in cross section, pointed, with several subdistal spines and long, stout, posteriorly-directed, curved setae.

Remarks. *Chlorodiella martensi* (Krauss, 1843) was described from South Africa and later synonymized with *Chl. laevissima* by Forest & Guinot (1961: 103). However, Forest & Guinot (1961) were unaware that the *Chl. laevissima* comprised three distinct lineages with slight differences in the G1—i.e., *Chl. martensi* is part of the *Chl. laevissima* complex (see Remarks for *Chl. laevissima* and *Chl. planapexa* sp. nov.).

Attempts to locate the holotype of *Menippe martensi* at Senckenberg Gesellschaft für Naturforschung and Staatliches Museum für Naturkunde Stuttgart were unsuccessful. It is unclear where Krauss' (1843) type specimens are housed. However, Krauss' (1843: 34, tab. 2, fig. 1) description and figure of the holotype does conform to the external morphology of members of the *Chl. laevissima* complex: *Chl. laevissima*, *Chl. planapexa* sp. nov., and *Chl. martensi*. The problem, then, is designating which of the three species it is, since Krauss did not illustrate the G1 of his specimen. Furthermore, all are present in the Western India Ocean. In Serène's (1984: 256, figs 171, 172) monograph on Indian Ocean xanthids, two "forms" of *Chl. laevissima* are presented with figures of their G1s—i.e., *Chl. laevissima* form *laevissima* and *Chl. laevissima* form *robusta*. The G1 figures correspond with the *Chl. laevissima* and *Chl. martensi* G1 morphology, respectively, to the exclusion of *Chl. planapexa* sp. nov. Serène (1984) stated that he chose the name "robusta" because the specimens he examined had relatively robust carapaces. This description fits Krauss' relatively robust holotype specimen. Furthermore, Krauss described the coloration of *Chl. martensi* as being brownish yellow with red bands on the claws and legs. Most *Chl. martensi* specimens examined for this study have a distinct pink or magenta coloration, whereas *Chl. planapexa* and *Chl. laevissima* usually have a red or brown carapace with white or yellow spots. However, two specimens of *Chl. martensi* (UF 9966, UF 15632) are a brownish yellow color, with a pink tint. Most specimens of these species have red or brown bands on the legs. Based on these data, Krauss' name, *Chl. martensi*, is attributed to the present species.

Distribution. *Chlorodiella martensi* is recorded from Hawaii and French Polynesia to Reunion Island and the Amirante Islands, Western India Ocean. The type locality is South Africa (Pl. 47B).

Chlorodiella nigra (Forskål, 1775)

Pls (11, 39B, 47C)

Cancer niger Forskål 1775: 89 (type locality: Red Sea).

Chlorodius niger Rüppell 1830: 20, pl. 4, fig. 7 [Red Sea]. — H. Milne Edwards 1834: 401. [Red Sea]. — Dana 1852b: 216 [Fiji; Tongatapu, Tonga; Wake Island; Upolu, Samoa; Sulu Sea and Mangsee, Philippines]; 1855, pl. 12, fig. 5 [Atlas]. — Stimpson 1858: 31 [List]; 1907: 50 [Ryukyu Is., Bonin Is., Japan; Tahiti(?)]. — Heller 1861b: 335 [Red Sea]. — Kossmann 1865: 34 [Red Sea]. — A. Milne-Edwards 1873: 214 [New Caledonia]. — Paul'son 1875: 35, pl. 6, fig. 4 [Red Sea]. — Miers 1880: 234 [New Guinea]; 1884: 215, 531 [Seychelles; Port Denison]. — De Man 1880: 174 [Djeddah, Saudi Arabia]; 1881: 98 [Red Sea]; 1887a: 32

[Elphinstone Island]; 1887b: 279 [Amboina and Pulo Edam, Indonesia]. — Richters 1880: 147 [Seychelles, Mauritius]. — Haswell 1882: 62 [Port Jackson and Darnley I., Australia]; 1902: [Ternate and Batjan, Indonesia]. — Whitelegge 1889: 227 [List]. — Henderson 1893: 361 [Toothukudi, Muttuwartu Par (Gulf of Mannar), and Rameshwaram, India]. — Ortmann 1893: 465 [Singapore; Amami Oshima, Japan; Fiji Is.; Upolu, Samoan Is.(?); Red Sea]; 1894b: 51 [Dar es Salaam, Tanzania]. — Zehntner 1894: 150 [Ambon I., Indonesia]. — Alcock 1898: 160 [Andaman Islands, Nicobar Islands, India; Mergui Archipelago, Myanmar; Makran Coast]. — Calman 1900: 11 [Thursday I. and Myer Reef, Torres Strait]; 1909: 705 [Christmas Island]. — Borradaile 1900; 587 [Funafuti; Rotuma]; 1902: 259 [Male, Fadifolu, Goifurfehendu, Felidu, North Male, and Minikoi Atolls, Maldives and Laccadives]. — Nobili 1905c: 487 [Seleo, W Sepik Province, Papua New Guinea]; 1906c: 262 [Eritea; Djibouti; Aden, Yemen]; 1907: 393 [Haorangi and Tikehau, Tuamotu Archipelago]. — Stimpson 1907: 50 (part) [Tahiti]. — Lenz 1910: 550 [St. Mary Island and Angongil Bay, Madagascar]. — Klunzinger 1913: 217 (121) pl. 6, fig. 10 [Red Sea]. — Laurie 1915: 447 [Sudan, Red Sea]. — Bouvier 1915: 97 [Mauritius]. — Gravier 1920: 467 [Diego-Suarez, Madagascar]. — Gravely 1927: 145, pl. 23, fig. 36 [Key]. — Vatova 1943: 20 [Somalia]. — Stephensen 1946: 156, fig. 38 d, e [Kharg I. and Bahrein I., Gulf of Iran].*Chlorodiella niger* (?)Rathbun 1906: 857 [Hawaiian Islands]; 1907: 46 [Rangiroa I.; Fakarava I.; Makemo I.; Bora Bora I.; Funafuti I.; Tari-Tari I.; Kusai(?), Carolines]. Laurie 1915: 447 [Sudan, Red Sea]. — Hale 1929: 70 [Dirk Hartog I., Australia]. — Balss 1938a: 52 [Aranuka, Apamama, Tamana, Tapitoea(?), Beru and Arari (?), Gilbert Is.; Niue and Nukufetau, Ellice Is; Jaluit, Marshall Is.; Viti Levu, Namuka, and Bau, Fiji]. — Sankarankutty 1962: 134, figs 30–31 [S Andaman Island, India].

Chlorodiella (*Chlorodius*) *niger* Laurie 1906: 405 [Trincomalee and Palk Bay, Sri Lanka]. — Edmondson 1923a: 17 [Palmyra I.; Fanning I.].*Chlorodiella nigra* Rathbun 1897: 157 [Nomenclature]; 1911: 225 [Salomon, Diego Garcia, Praslin, Coetivy]; 1923: 108 [North West Island, Australia]. — Grant & McCulloch 1906: 12 [Mast Head I., Australia]. — Balss 1924: 10 [Golf von Suez, Tor, Ras el-Millan, Senafir, Koseir, Berenice, Djeddah, Lidth?, Dahlak, Massaua, Daedalus Reef, Hamfela(?), Zebejir(?), Sarso I., Akik Segir(?), Mersa Haleib(?), Perim, St. Johns I. (?), Mersa Scheikh(?), Ravaya(?)]. — De Man 1929a: 1 [Pulau Berhala, Malaysia]; 1929b: 4 [Pulau Berhala, Malaysia]. — McNeill & Ward 1930: 383 [Port Jackson, Australia]. — Montgomery 1931: 441 [Long I., Pelsart I., and Wooded I., Abrolhos Is.]. — Ward 1932: 249 [Heron Island, Hoskyn Island, One Tree Island, North West Island and Fairfax Island, Australia]. — Gordon 1934: 50 [Banda Neira, Indonesia]. — Shen 1936: 67 [Hainan Is.]. — Miyake 1936: 508 [Yaeyama, Japan]. — Sakai 1936b: 166 [Palau Islands]; 1939: 508, pl. 97, fig. 1 [Loo Choo, Japan]; 1965: 150, pl. 75, fig. 2 [Sagami Bay, Japan]; 1976: 465, pl. 166, fig. 1 [Sagami Bay, Yoron I., Ishigaki I., and Taketomi I., Japan]. — Chopra & Das 1937: 402, pl. 6, fig. 2 [Mergui Arch.]. — Ramadan 1936: 32 [Ghardaqa, Egypt, Red Sea]. — Monod 1938: 132 [Bay of Suez]. — Lin 1949: 23 [Taiwan]. — Barnard 1950: 213 [Natal, South Africa]; 1955: 29, fig. 10 [Delago Bay, South Africa(?)]. — Holthuis 1953: 15 [Onotoa, Gilbert Islands]. — Guinot 1958a: 180 [Mayotte]; 1962b: 238 [Sarso Island, Saudi Arabia]; 1964a: 12 [Massawa and Entaentor, Eritrea]; 1964b [Abulat, Saudi Arabia]: 69; 1967: 262 [list]. — Forest & Guinot 1961: 95, figs 87–89, 97 a, b [Tahiti]. — Sankarankutty 1966a: 351 [Manoli I., India]; 1966b: 50 [Mauritius]. — Chang 1963: 99 [Pescadores, Taiwan]. — Michel 1964: 24 [Mauritius]. — Serène 1968: 81 [list]; 1977a: 51 [Seychelles]; 1984: 258–259, fig. 168, pl. XXXVI B [Nosy

Be and Tulear, Madagascar; Ile Europa]. — Serène *et al*. 1976: 18 [Ambon I., Indonesia]. — Takeda & Nunomura 1976: 74 [Kokopo (near Rabaul), New Britain; Guadalcanal Island (Honiala), Solomons; Saddle Island, Torres; Ilot Maitre, Ile des Pins, and Poum, New Caledonia]. — Takeda & Miyake 1976: 108 [Ogasawara Is., Japan]. — Peyrot-Clausade 1977a: 26 [Tulear, Madagascar]; 1977b: 213 [Moorea]. — Chen & Lan 1978: 268, figs 1, 7 (6–7), pl. 1, fig. 1 [Xisha Islands]. — Ribes 1978: 126 [Reunion I.]. — Takeda 1978: 40 [Kyushu, Japan]. — Kensley 1981: 44 [List]. — Garth & Kim 1983: 687 [Little Santa Cruz I. and Burias Island, Philippines]. — Dai *et al*. 1986: 315, pl. 45(5), fig. 169(2) [Review]. — (?)Titgen 1987: 107 [Hawaii]. — Dai & Yang 1991: 339, pl. 45(5), fig. 169(2) [Review]. — Davie 2002: 519 [List]. — Coles *et al*. 2002b: 137 [List]. — Coles *et al.* 2008: 62 [List].

Cancer clymene Herbst 1801: 41, tab. LII, fig. 6 [East Indies].

Xanthias clymene Sakai 1999: 34, pl. 18A [List].

Chlorodius nebulosus Dana 1852b: 214 [Sulu Sea]; 1855: pl. 12, fig. 3a–b [Atlas].

Chlorodius depressus Heller 1861b: 338 [Red Sea] (according to De Man 1880).

Chlorodius hirtipes Adams & White 1848: 40, pl. 11, fig. 4 [Philippines].

Chlorodius rufescens Targioni-Tozetti 1877: 43, pl. iv, figs. 6-8, 10-12, 14, 18 [Java].

Chlorodiella xishaensis, Serène 1984: 258, pl. XLIII F (part) [Madagascar]. (not *Chlorodiella xishaensis* Chen & Lan, 1978)

Chlorodiella spinimera Dai, Cai & Yang 1996: 256, fig. 9.

Material examined. *Red Sea:* male, 16.85 × 11.05 (SMF 7161), Rotes Meer, Eritrea, Massaua; Tropicarium des Palmengartens in Frankfurt am Main. — 5 males, largest = 18.30 × 11.75 (SMF 37860), Sudan, Al Bahr al Ahmar, Sanganeb-Atoll 28 km NE Port Sudan, SAN-133, 1 m Tiefe, aus lebenden, Stylophora, coll. 25 September 1992. — 2 males, largest = 17.00 × 11.00, 2 females (SMF 6898), Golf von Suez, Rotes Meer, Tropicarium des Palmengartens in Frankfurt am Main, coll. 22 December 1960. — 1 male, 7.0 × 4.6, 1 female, 13.1 × 8.5 (USNM 101094), in violet branching coral, Eastern Desert Governorate, Egypt, Ain Sokhna, Gulf of Suez, coll. C. Yunker, 12 July 1957. — 1 female, 8.7 × 6.0 (UF 36712*), Stn. SAFA-013, 17.9902° 41.6627°, 0–1 m, silty near shore sand and rocks, Al Qahmah, Coast Guard Harbor, Saudi Arabia, coll. G. Paulay & P. Norby, 7 March 2013. — 1 male, 9.7 × 6.5 (UF 36711*), Stn. SAFA-013, 17.9902° 41.6627°, 0–1 m, silty near shore sand and rocks, Al Qahmah, Coast Guard Harbor, Saudi Arabia, coll. G. Paulay & P. Norby, 7 March 2013.

Djibouti: 1 male, 16.6 × 11.3 (UF 32887), Stn. DJRS-018, 11.51875° 42.6638°, 0–1 m, rubble, intertidal to shallow subtidal shore fringe, Bay of Ghoubbet, E side, Djibouti, coll. J. M. Rose & J. L. Rose, 1 October 2012. — 1 female, 8.4 × 5.4 (UF 37894), Stn. DJRS-007, 11.976° 43.365°, 8–13 m, in dead *Pocillopora*, reef slope, NE Gulf of Tadjoura, E of Obock, Djibouti, coll. G. Paulay, 29 September 2012.

Gulf of Aden: 1 female, 12.9 × 8.9 (USNM 19036), Gulf of Aden, coll. L. McCormick, Glen Island Museum, Acc. No. 29431.

Persian Gulf: 4 males, largest = 21.85 × 13.85, 1 female (SMF 37968), Vereinigte Arabische Emirate, Abu Dhabi, Al Bizm al Gharbi, NW-Spitze des Riffs (“Dead Dhow Reef”), UAE95-02 (24°22.957’ N 53°4.081’ E - 24°22.957’N 53°4.081’E) 3–9m Tiefe, Riff u. a. aus *Porites*, *Platygyra*, *Acropora*, teilweise mit Algen bewa, coll. M. Apel, 11 June 1995 — 1 female, 13.40 × 12.15 (SMF 37971), Vereinigte Arabische Emirate, Sharjah, Lulayyah, Hafen, UAE95-17 (25°23’N 56°22’E - 25°23’N 56°22’E) 0–3 m

Tiefe, im Hafenbecken, an Kaimauer, auf Felsen und unter Steinen im Hafenbeck, coll. M. Apel, 27 June 1995. — 1 male, 15.25 × 11.65 (SMF 37972), Vereinigte Arabische Emirate, Sharjah, ca. 500–800 m N von Lulayyah Port, UAE95-26 (25°24’N 56°22’E - 25°24’N 56°22’E) 3–5 m Tiefe, Acropora-Riff mit einigen wenigen anderen Korallen (*Porites*, *Platygyra*), coll. M. Apel, 2 July 1995. — 3 males, largest = 17.45 × 11.85, 1 ovigerous female (SMF 37970), Persischer Golf, Saudi-Arabien, Ash Sharqiyah (Eastern Province), Offshore-Inseln, Jana Island, S-Seite (27°22’N 49°54’E) 10–20 m Tiefe, in Korallen und Korallenschutt, coll. M. Apel, 31 May 1995.

Arabian Sea: 1 male, 21.15 × 14.20 (UF 17948*), BOMAN-502, GP-Loc-814, 1–3 m, silty back reef mix soft bottom & resilient corals, under rocks, SSE tip of Bar Al Hikman Peninsula, Oman, coll. V. Bonito *et al.*, 24 January 2005. — 1 female, 11.5 × 7.7 (UF 18021), Stn. GP-Loc-815, 1 m, top of *Montipora* reef margin, SSE Tip of Bar Al Hikman Peninsula, Oman, coll. V. Bonito *et al.*, 24 January 2005.

Madagascar: 1 male, 15.10 × 10.40 (UF 14214), MGNW-20, -13.4244° 48.3642°, 3–6 m dive, off ENE side of Nosy Vorona, Madagascar, coll. G. Paulay, 15 May 2008. — 1 ovigerous female, 11.25 × 7.90 (UF 14288*), NBE-1333, MGNW-21, 4 m, -13.4244° 38.3642°, broken reef, rubble, sand on shallow slope, extracted from large dead *Porites rus*, off ENE side of Nosy Vorona, Madagascar, coll. A. Anker *et al.*, 15 May 2008. — 14.65 × 10.30 (UF 14275*), NBE-0974, MGNW-21, 4 m, -13.4244° 38.3642°, broken reef, rubble, sand on shallow slope, extracted from large dead *Porites rus*, off ENE side of Nosy Vorona, Madagascar, coll. A. Anker *et al.*, 15 May 2008. — 1 male, 13.6 × 9.4 (UF 14606*), Stn. MGNW-38, -13.42923° 48.36398°, 1–6 m, lagoonal fringing reef slope with sand and rubble, Trois Freres islet(?), near Nosy Be, N end of islet, Madagascar, coll. A. Anker *et al.,* 20 May 2008.

Reunion Island: 1 female, 7.10 × 5.20 (UF 12650*), BREU-0224, SWIO-2, 0–1 m, -21.1072° 55.2498°, fringing reef moat, ex *Pocillopora damicornis*, Saint-Paul, Varangue du lagon, Reunion Island, Mascarene Islands, coll. H. Bruggemann *et al.*, 6 August 2007.

Seychelles: 1 female, 7.1 × 4.7 (USNM 41251), reef, Praslin, Seychelles, coll., H.M.S Sealark, 1905, Acc. No. 51720. — 1 male, 9.8 × 6.4, 2 females, 16.6 × 10.6 – 17.9 × 11.7 (USNM 41251), Coetivy, Western Indian Ocean, coll. H.M.S Sealark, 1905.

Thailand: 5 males, 9.6 × 6.5 – 14.1 ×9.6, 1 female, 13.5 × 8.6 (USNM 184255), Goh Phuket, Thailand, Andaman Sea, coll. Gallardo, 4 February 1966. — 4 males, 8.1 × 5.7 – 12.3 × 8.3, 3 females, 10.6 × 6.9 – 11.3 × 7.8, 2 ovigerous females, 9.2 × 6.4 – 12.1 × 8.1, 1 juvenile (USNM 1191860), Koh Tao, Andaman Sea, Thailand, coll. H. Smith, 24 September 1928. — (?) 1 male, 10.8 × 7.1, 1 ovigerous female, 12.1 × 8.2 (USNM 1191842), in coral, shoal water, Koh Tau, Siam, coll. H. Smith, 24 September 1928, Acc. No. 104216.

China: 1 male, 13.6 × 9.2, 1 female, 15.6 × 9.8 (USNM 1191890), Shanghai, China, coll. E. Deschamps.

Australia: 1 male, 19.1 × 12.3 (UF 17865*), Stn. AUST-ST-000, Lizard Island, Queensland, Australia, coll. February 2009. — 1 female, 12.8 × 8.4 (UF 24753*), Stn. HI09-010, -23.43321667° 151.93375°, 8–10 m, in rubble, back reef, bommies on sand, *Acropora* patches, Heron Island, First Point, North Heron Reef, Queensland, Australia, coll. 12 November 2009. — 1 male, (ZRC 2010.0376*), Ningaloo Reef, Australia. 1 male, 13.6 × 9.6, 1 female, 12.2 × 8.3 (USNM 81390), Mer, Murray Islands, Torres Strait, Australia, coll. H. Clark, October 1913. — 2 males, 8.8 × 5.9 – 10.9 × 7.1, 1 female, 6.2 × 4.2 (USNM 1191843), coral reef, Yirrkala, Australia, coll. R. Miller, 26 August 1948, C13-C17, Acc. No. 178 294. — 1 male, 16.4 × 10.8, 3 ovigerous females, 10.60 × 6.8 – 13.3 × 8.5 (USNM 134523), Yirrkala Mission, Arnhem land, Gulf of Carpentaria, Northern Territory, Australia, coll. 26 August 1948.

Indonesia: 1 male, 11.5 × 8.0 (ZRC 2013.1605), Stn. BL11-004, BALI-0206, 0–20 cm, -8.71348° 115.2516°, under rock, hand collected, night intertidal, rocky substrate, hard exposed substrate with sandy patches, scattered coral, sea grass, exposed (low tide), close to breakers, approx. 300 meters from shore, Closest beach from Rama Villas, Sanur Beach, Bali, Indonesia, coll. 19 June 2011. — 1 female, 8.0 × 5.6 (USNM 1191887), Poeloe Toekus Island (?), Indian Ocean, coll. H. Keller, Acc. 87 355. — 1 male, 8.4 × 5.8 (USNM 134522), coral head, Lembek Strait, Celebes, Indonesia, coll. A. Herre, 21 June 1929.

Philippines: 2 males, largest = 11.33 × 7.88, 8 females (AMNH 8070), Gulf of Davao, Philippines, June 20, 1936. — 1 male, 14.55 × 10.16, 1 female (AMNH 7648), Gulf of Davao, Philippines, June 14, 1936. — 1 male, 18.98 × 12.88 (AMNH 7905), Padada Beach, Gulf of Davao, Celebes Sea, Philippines, coll. G. Oesch, July 16–19, 1936. — 1 male, 19.00 × 12.45 (ZRC 2013.0565*), B22, 15–20 m rubble on mixed bottom, 9°29.4'N 123°56.0'E, Pamilacan Island, coll. 24 June 2004. — 3 males, largest = 11.60 × 8.05, 7 females, 4 juveniles (ZRC 2012.0566), B22, 15–20 m rubble on mixed bottom, 9°29.4'N 123°56.0'E, Pamilacan Island, coll. 24 June 2004. — 6 males, 6.7 × 4.6 – 15.4 × 10.6, 6 females, 5.5 × 3.9 – 11.4 × 7.8, 2 ovigerous females, 12.5 × 8.9 – 15.1 × 10.3 (USNM 65221), shore, coral head, Marongas Island, Philippines, coll. U.S. Bureau of Fisheries, Albatross Philippine Expedition, 10 February 1908. — 2 males, 7.2 × 5.0 – 12.1 × 8.4 (USNM 65275), Tinakta I., Tataan Passage, Tawitawi I., Sulu Archipelago, Philippines. — 3 males, 10.2 × 7.2 – 13.5 × 9.6, 2 females, 9.7 × 6.9 – 10.5 × 7.2 (USNM 1191866), Little Santa Cruz I., Mindanao I., Zamboanga del Sur, Philippines, coll. Philippines Expedition, Albatross, 26 May 1908.

Japan: 1 female, 7.6 × 5.6 (UF 26996*), Stn. GUOK10-St-071, 26.21218° 127.664291°, 1–8 m, silty harbor, river mouth, wharfs, Okinawa, Naha Harbor, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 16 July 2010. — 1 female, 7.7 × 5.4 (UF 26946*), Stn. GUOK10-St-067, 24.421202° 123.802599°, 0–1 m, mostly under rocks, reef at low tide, Iriomote, Uehara, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 10 July 2010.*Mariana Islands:* 1 male, 30.00 × 19.30 (ZRC 2000.0688), Guam, coll. J. Starmer, April 2000. — 1 male (damaged) (UF 2770), ZZZ-087511, 2–5 ft, among coral rubble and rocks, Apra Harbor, Drydock Shoal, Guam, Mariana Islands, coll. H. Conley, 15 June 2002. — 1 male, 30.20 × 19.00, 2 females (UF 877), UGML-0440, GP-393:20-21, 25, display tank, University of Guam Marine Laboratory, Mangilao, Guam, Mariana Islands, coll. J. Starmer, 1 April 1997. — 1 male, 12.0 × 8.0, 1 females, 10.5 × 7.0 (USNM 1191852), Saipan, coll. A. Herre, 7 October 1933, 136/895. — 1 male, 30.6 × 19.7 (USNM 1005160), 40 ft, under coral, Tanguisson, Guam, coll. O. Odinetz, June 1981. — 1 male, 13.0 × 8.6 (UF 3014), Stn. ZZZ-087534, 3–10 ft, under rocks and among coral rubble, E edge of Western Shoal, Apra Harbor, Guam, coll. H. Conley, 18 May 2002.

Caroline Islands: 1 male, 13.3 × 8.6, 2 females, 10.6 × 7.1 – 11.0 × 7.5 (USNM 33319), Kusaie, Kosrae, Carolines, coll. 1900, Acc. No. 45786. — 1 male, 17.9 × 12.0, 1 female, 10.9 × 7.4 (USNM 1191877), Stn. 10, Palau Island, coll. 1955, Acc. No. 206221, #814. — 4 males, 5.0 × 3.3 – 8.5 × 5.4 (USNM 1191888), reef, *Pocillopora*, Kapingamarangi lagoon, Pohnpei, coll. C. Hand, 20 July 1954, Acc. No. 205840. — 2 males, 13.3 × 8.7 – 17.2 × 11.0 (USNM 106526), Stn. 786, lagoon reef at Katelu benjo, Ifaluk Atoll, coll. Fourth Pacific Atoll Survery Team, Pacific Science Board, 31 October 1953. — 1 male, 7.70 × 5.05 (UF 3880*), BPAL-083, 10 m, 7.3043° 134.4542°, nestled among branches of *Acropora*, rocky islets NE off Ngeryktabe Island, Palau, coll. G. Paulay, 5 March 2003.

Solomon Islands: 1 male, 9.20 × 6.35 (UF 3320*), ZZZ-087899, 3–5 ft, among coral and rocks, Near JFK Island, Ghizo Island, Solomon Island, coll. H. Conley, 12 February 2002. — 1 male, 16.85 x 11.89 (AMNH 6347), Choiseul Bay, Choiseul Island, British Solomon Islands, coll. W. Eyerdam, September 1929. — 1 male, 26.5 × 17.5 (USNM 1191849), Cape Tarakina, Bougainville, Solomon Islands, coll. D. Johnson, 4 August 1944. — 1 female, 16.50 × 10.70 (UF 3338*), ZZZ-87898, 3-6 feet, under rocks and among coral, near Ghizo City, Ghizo Island, coll. H. Conley, 16 February 2002. — 3 males, 13.7 × 8.8 – 17.5 × 11.1, 4 females, 11.5 × 7.5 – 17.5 × 11.6 (USNM 1138270), Sikaiana Atoll, NE of Malaita Island, Solomon Islands, coll. 12 May 1933.

New Caledonia: 1 ovigerous female, 16.9 × 11.5 (UF 37977*), NewC13-258, NEST 12, 0–2 m, -22.3938° 166.883°, Back reef to reef top, dense coral, some rubble, Prony Bay, New Caledonia, coll. N. Evans, 4 November 2013.

Marshall Islands: 1 female, 14.7 × 9.4 (USNM 1191848), Bikini Atoll, coll. M. Johnson, May 1946, 172 586. — 1 male, 8.7 × 5.8 (USNM 1191850), Arno Atoll, coll. R. Hiatt, Acc. No. 195 038. — 1 female, 13.3 × 8.4 (USNM 1191889), in and under coral, Kabbenbock Island, Jaluit, coll. 20 October 1960, Acc. No. 232355, R6-60.

Wake Island: 1 female, 9.65 × 6.35 (UF 8576*), 0–2 ft, 19.305° 166.6002°, lagoon, Wake Island, coll. V. Bonito, 31 November 2005 – 1 Decemeber 2005.

Gilbert Islands: 6 males, 5.4 × 3.5 – 12.6 × 8.1, 2 females, 6.5 × 4.2 – 12.4 × 7.6 (USNM 94013), limemud and limesand with low scattered dead and living coral patches, about 13,400 ft S 75° W from Akiaki Maneaba in the deep central part of the lagoon, Onotoa, Gilbert Islands, coll. P. Cloud, 25 August 1951. — 1 female, 8.6 × 5.6 (USNM 94014), 1–9 ft, reef stretch, from reef patch, lagoon, about 1 mi. S. 32° W from Tekawa church at lagoon margin of S end of Aon te Baba reef stretch, Onotoa, Gilbert Islands, coll. P. Cloud, 31 July 1951.

Samoan Islands: 1 male, 9.78 x 6.92, 1 female (AMNH 7587), Western Samoa, 17 October 1936. — 1 male, 12.46 x 8.57 (AMNH 7607), Western Samoa, 15 October 1936. — 1 male, 11.0 × 7.6, 3 females, 9.5 × 6.6 – 10.6 × 7.5 (USNM 23139), Samoa, coll. C. Eliot, Acc. No. 35615. — 1 female, 7.00 × 5.10 (UF 9533*), SMOFU-001, hand collected, in/on *Pocillopora damicornis*, lagoonal reef, Ofu Unit, American Samoa National Park, Ofu Island, American Samoa, coll. S. McKeon, Feb–Apr 2007. — 8 males, 9.7 × 6.7 – 15.5 × 10.7, 2 females, 10.4 × 7.4 – 15.8 × 10.9 (USNM 1191863), outer coral reef at low tide, Apia, Samoa, coll. 1 July 1902.

Kiribati: 1 female, 11.14 x 7.47 (AMNH 7605), Penrhyn Island, Oceanica, 18 September 1936. — 1 male, 17.4 × 11.2 (USNM 1191854), Canton Island, coll. L. Schultz, U39-33. — 4 males, 5.0 × 3.3 – 12.5 × 8.4, 2 females, 10.9 × 7.4 – 12.3 × 7.9 (USNM 1191861), inner lagoon, Fanning Island, coll. F. Baker & C. Baker, 16 December 1913. — 1 male, 14.1 × 9.0, 2 females, 11.1 × 7.4 – 18.8 × 11.8 (USNM 33317), shore-reef, Tari Island, coll. Bureau of Fisheries, 6 January 1900. — 3 males, 10.0 × 6.8 – 15.8 × 10.3, 8 females, 7.2 × 4.9 – 14.3 × 9.2 (USNM 1191845), inside coral, W lagoon, Kanton I., Kiribati, coll. C. Ely, Jan 1942.

Hawaiian Islands: 2 males, 13.4 × 8.5 – 16.6 × 10.9 (USNM 13916), Honolulu, Sandwich Islands, coll. before February 1889.

Society Islands: 1 female, 11.20 × 7.40 (UF 10004*), BMOO-479, GP-Loc-865, 0–2 m, -17.5311° -149.9053, fringing reef under little terrigenous influence, from *Pocillopora* colony, inner fringing reef inshore and N of

Tauotaha Pass, Moorea Island, Society Islands, French Polynesia, coll. C. McKeon & G. Paulay, 22 June 2006. — 2 males, 6.1 × 4.0 – 6.7 × 4.4, 2 females, 8.8 × 5.7 – 11.9 × 7.8 (USNM 33316), fringing reef, Bora Bora, Society Islands, coll. U.S. Fish Commission, Steamer Albatross, 17 November 1899. — 4 males, 5.2 × 3.5 – 12.0 × 8.1, 1 female, 6.4 × 4.3 (USNM 1191859), head of Bai de Maroe, Huahine, coll. Bredin Expedition, 30 April 1957, #84a-57, Acc. No.213 821. — 1 male, 9.8 × 6.5 (USNM 1191872), reef NW of Motu Uta Island, Papeet, Tahiti, coll. 19 April 1957, Acc. No. 213 821, #40-57. — 1 male, 9.8 × 6.3, 2 females, 6.2 × 3.6 – 6.9 × 4.5 (USNM 1191876), Uturoa, Raiatea, Society Islands, coll. 28 April 1957, Acc. No. 213821, 75-57.

Tuamotu Islands: 1 male, 11.65 × 7.55 (UF 18513), Bacchet-001, reef flat, Makemo Atoll, Tuamotu Islands, French Polynesia. — 1 male, 18.4 × 11.6, 2 females, 5.3 × 3.5 – 11.6 × 7.3 (USNM 1191857), 50 ft, coral, lagoon, Tikahau Atoll, coll. 12 April 1957, 18-57, Acc. No. 213821.

Diagnosis. Carapace (Pl. 11B) transversely hexagonal, relatively broad, ca. 1.5 broad as long; dorsal surface smooth, lateral regions marked by relatively high elevations, 2M and 3M poorly defined, posterior border of 3M with H-shaped groove. Front (Pl. 11C) broad, submedian lobes convex or sinuous, separated by V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low, obtuse; teeth 1–3 low, obtuse, triangular (cornuted in smaller specimens). Anterolateral angle of basal antennal segment slightly or not produced, mostly hidden behind inner suborbital projection. Pterygostomial region with plumose setae diagonally from posterior to lateral surface; setae sometimes few or absent on mesial posterior margin, more numerous laterally. Chelipeds (Pl. 11E, F) unequal, long, tips of fingers hollowed, spoon-like; outer surface of chelae smooth; major cheliped about twice as long as length of carapace; major chela propodus almost as long as width of carapace. Ambulatory legs (Pl. 11A) with extensor margin of carpus and propodus covered with long, plumose setae; extensor margin of merus lacking or with few minute distal spines; tip of dactylus bifid; distal pigmented spine slightly longer than curved tip. Male thoracic sternum (Pl. 11D) with press button located on sternite 5, 2/3 way to suture between sternites 4, 5. Male abdomen (Pl. 11D) long, narrow, with sutures between somites 3/4 and 4/5 slightly indicated, appearing smooth to naked eye; telson triangular, longer than broad. G1 (Pl. 39B) curving ventrally 3/4 way to tip, lateral margin with row of subdistal stout, simple, proximally directed setae; apical lobe longitudinally hollowed, anterior margin convex.

Remarks. *Chlorodius niger* (Forskål, 1775) was designated as the type species of *Chlorodius* by H. Milne Edwards (1834). Later, Rathbun (1897a) changed *Chlorodius* to *Chlorodiella* because *Chlorodius* is a junior synonym of *Atelecyclus* Leach, 1814. Since *Chlorodius* was the type genus of Chlorodiellinae, *Chlorodiella* assumed assignment as type genus of the subfamily. The stability of this name is important.

The taxonomic history of *Chlorodiella nigra* is complicated, with six junior synonyms. The confusion is likely due to the variability of characters in this species which have historically been used to distinguish between members of *Chlorodiella*—e.g., anterolateral teeth and carapace regions. Forest and Guinot (1961: 96, 98), treated three of the junior synonyms (*Chlorodius nebulosus* Dana 1852b, *Chlorodius depressus* Heller 1861, *Chlorodius hirtipes* Adams & White 1848), and mentioned another without explanation (*Chlorodius rufescens* Targioni-Tozetti 1877). Based on the examination of the holotype specimen of *Chlorodius hirtipes* and the original descriptions and figures of *Chlorodius nebulosus, Chlorodius depressus*, and *Chlorodius rufescens*, the morphology of these species agrees with their synonymy. Of the remaining two names, *Cancer clymene* Herbst 1801, was tentatively assigned to *Xanthias* by Sakai (1999: 34), but Ng *et al*. (2008) regarded it as a junior synonym of *Chl. nigra*. The type specimen of *Cancer clymene* in Sakai (1999: pl. 18A) appears morphologically congruent to *Chl. nigra*.

The synonymy of *Chlorodiella spinimera* Dai, Cai & Yang, 1996, needs further explanation. The description and figures of this species closely characterize a juvenile *Chl. nigra*. The authors state, "This new species is similar to *Chlorodiella niger* (...) but it may easily be distinguished from the latter in the last 3 anterolateral teeth spine-formed, merus and carpus of cheliped each with 2 spines on anterior border of (merus) and inner distal angle of carpus: larger manus with big gap between two fingers; meri of ambulatory leg with serrated teeth on anterior border." However, juvenile or immature specimens of *Chl. nigra* generally have spiniform anterolateral teeth, a cheliped carpus with two spines, gaping major chelar fingers, and serrated meri of the ambulatory legs (e.g., ZRC 2013.0566, ZRC 2010.0376, ZRC 2010.0377, ZRC NING 0161, and ZRC NING 0156). As for the cheliped merus, the anterior margin of juvenile or immature *Chl. nigra* specimens usually only possesses one emergent spine, not two, and many minute spines or conical granules. However, some of these conical granules may be more emergent than the others—rarely, only one conical granule is emergent and is positioned next to the large emergent spine (e.g., ZRC 2013.0566). It is unclear whether this is the form of the type specimens of *Chl. spinimera*. The specimens were unavailable for examination, and the figure of the cheliped [Dai *et al.* 2006: fig. 9(2)] only illustrates the dactylus, propodus and carpus. It is clear, however, that the G1 of immature *Chl. nigra* specimens at the right level of development (e.g., ZRC 2010.0376) are strikingly similar to that of *Chl. spinimera* [Dai *et al*., 1996: fig. 9(5, 6)]. *Chlorodiella spinimera* is regarded as a junior synonym of *Chl. nigra*.

Chlorodiella nigra is easily distinguished from its congeners by the combination of the following features: large size, long chelipeds, distinct anterolateral regions of the carapace, and a unique G1 (Pl. 11A, B, E, F, 39B). One unique character is worth mentioning as it is not found in most members of the family Xanthidae. In *Chlorodiella nigra*, the sutures between male abdominal segments 3/4 and 4/5 are usually indicated by a faint, shallow line. This feature is contrary to the currently accepted definition of Xanthidae.

Chlorodiella nigra is closest to *Chl. xishaensis* in having a similarly shaped carapace with raised lateral regions, a G1 that is bent 3/4 the way to the tip, a G1 tip that is spatulate and longitudinally hollowed, and ambulatory legs with numerous plumose setae. However, *Chl. nigra* is generally much larger in size. It also has a carapace with a smooth surface and more distinctly defined borders of the anterolateral regions [versus granular and less defined borders in *Chl. xishaensis* (Pl. 15B)], longer chelipeds [versus shorter in *Chl. xishaensis* (Pl. 15E, F)], a relatively longer telson with a broader tip [versus shorter with a narrower tip in *Chl. xishaensis* (15D)], and a G1 with a more angular bend and rounded tip with a convex anterior margin [versus less angular bend with a pointed tip in *Chl. xishaensis* (Pl. 39D)].

Distribution. *Chlorodiella nigra* is recorded from the Red Sea and Western Indian Ocean to the Hawaiian Islands and French Polynesia (Pl. 47C). The species has been recorded in the Hawaiian Islands by many authors (e.g., Rathbun 1906, Edmondson 1962; see Castro 2012). However, Titgen, (1987) reported that these records were incorrect, the previously reported specimens were misidentified *Chl. cytherea* or *Chl. laevissima* specimens, and there are no known collections of specimens of *Chl. nigra* from the Hawaiian Islands. This may be true, but one lot of two male specimens identified as *Chl. nigra* has been located at the National Museum of Natural History, Smithsonian Institution (USNM 13916). The specimens, collected sometime before 1889, have apparently been rotten, dried and subsequently stored in ethanol, but are clearly *Chl. nigra*. It would be interesting to re-examine old and new collections to investigate the status of this species in the Hawaiian Islands.

Chlorodiella ohshimai Miyake & Takeda, 1976

Pls (13, 47D)

Chlorodiella ohshimai Miyake & Takeda 1967: 295–297, figs 1a–c, 2a–d [type locality: Ishigaki Island, Okinawa, Japan]. — Serène 1968: 81 [List]. — Sakai 1976: 466 [List].

Material examined. *Japan:* Holotype male, 12.55 × 7.85 (ZLKU 2613), Yaéyama Expedition II, Ishgaki-jima Island, Yaéyama Group, Ryukyu Islands, coll. H. Ohshima *et al.*, 27 July 1933.

Diagnosis. Carapace (Pl. 13A) transversely hexagonal, ca. 1.6 broad as long, dorsal surface smooth, anterolateral and posterolateral regions minutely granulose, regions undefined. Front (Pl. 13D) broad, submedian lobes slightly convex, lobes separated by minute notch. Anterolateral margin with only 2 discernible teeth excluding outer supraorbital tooth; teeth 1 and 2 conjoined, forming convex lobe; tooth 3 acute, pointed, cornute, anteriorly directed; tooth 4 minute with slight, granular transverse ridge on dorsal surface. Anterolateral angle of basal antennal segment slightly or not produced, mostly hidden behind inner suborbital projection. Pterygostomial region without setae. Minor cheliped unknown. Major cheliped (Pl. 13C) relatively long; outer surface of chela smooth. Ambulatory legs with sparse long, simple setae, increasing in number from merus to dactylus; extensor margin of merus lined with relatively long, distally directed spines, especially distally; tip of dactylus bifid, distal pigmented spine slightly longer than curved tip. Male thoracic sternum (Pl. 13B) with press button located on sternite 5, 2/3 way to suture between sternites 4, 5. Male abdomen (Pl. 13B) long, narrow, smooth; somites 3 to 5 fused without discernible sutures except slight lateral notch on suture 4/5; telson longer than broad, tip rounded. G1 tip pointed, spatulate, longitudinally hollowed, with row of subdistal setae and short spines.

Remarks. This species is easily distinguished from its congeners by its anterolateral margin which has a lobe followed by 2 teeth—the first is larger, cornuted, and anteriorly directed; and the last is minute and triangular (Pl. 13A) (vs. 3 or 4 anterolateral teeth in other species). Only one specimen is known, the holotype, from Ryukyu Islands, Japan, which was examined for this study. The male G1 was not available for examination, but the structure is illustrated well in the original description (Miyake & Takeda, 1967: fig. 2a–d). Based on this figure, the G1 of *Chl. ohshimai* is identical to that of *Chl. xishaensis* Chen & Lan, 1978. However, these two species differ by the aforementioned features of the anterolateral margin (*Chl. xishaensis* has four distinct anterolateral teeth excluding the outer supraorbital tooth) and *Chl. ohshimai* has a relatively broader carapace and ambulatory legs simple setae (vs. a relatively narrower carapace and ambulatory legs with numerous plumose and simple setae in *Chl. xishaensis*).

Distribution. Only one specimen has been recorded, the holotype, from Ishgaki-jima Island, Yaéyama Group, Ryukyu Islands, Japan (Pl. 47D).

Chlorodiella quadrilobata Dai, Cai & Yang, 1996

Pls (14, 48A)

Chlorodiella quadrilobata Dai, Cai & Yang 1996: 255–256, fig. 8. [type locality: Spratly Islands]. — Ng *et al.* 2008: 196 [List].

Diagnosis. Carapace (Pl. 14B) transversely hexagonal, ca. 1.4 broad as long, dorsal surface smooth, regions undefined. Front (Pl. 14C) broad, arched, submedian lobes separated by shallow notch. Anterolateral margin with 3 teeth excluding exorbital tooth; teeth 1, 2 lobular; tooth 3 rounded. Basal antennal segment "standing in orbital hiatus" (Dai *et al*. 1996: 255). Chelipeds (Pl. 14E, F) unequal, tips of fingers hollowed, spoon-like; outer surface of chelae smooth. Ambulatory legs (Pl. 14A) slender, smooth; last three segments with fine setae; tip of dactylus bifid. Male abdomen (Pl. 14D) long, narrow; somites 3 to 5 fused; telson subtriangular, tip rounded. G1 tip truncate with blunt spines.

Remarks. *Chlorodiella quadrilobata* is easily distinguished from other members of the genus by its 3 lobular anterolateral teeth (Pl. 14B) (versus 1 to 4 triangular teeth in other species). Furthermore, the truncated G1 is distinct. These features potentially warrant the removal of this species from the genus. However, only three specimens are known, the type series from the Spratly Islands, which were unavailable for examination. Photos of the type series were obtained, although certain features could not be ascertained. The present diagnosis reflects information gleaned from these photos and the original description. Further examination of the type series is necessary to properly assess the status of this species.

Distribution. This species is only recorded in its original description from the Spratly Islands (Pl. 48A).

Chlorodiella xishaensis Chen & Lan, 1978

Pls (15, 39D)

Chlorodiella xishaensis Chen & Lan 1978: 271, 285, figs 6, 7 (10–11), pl. 2 fig. 6 [type locality = Xisha Islands]. — Serène 1984: 258, fig. 173, pl. XLIII E (part) [Philippines]. — Dai *et al.* 1986: 319, fig. 169 (4), pl. 45 (8) [List]. — Dai & Yang 1991: 338, 342, fig. 169 (4), pl. 45 (8) [List]. — Davie 2002: 519 [List]. — Ng *et al*. 2008: 196 [List].

Material examined. *Australia:* 2 males, intact specimen = 5.9 × 4.0, 1 female (QM W23054), 13 m, 23.53.2 S, 152.25.4 E, infauna, dead branching coral, reef slope, marine, Lady Musgrave Island, Capricorn-Bunker Grp, NE edge, ME.QLD, coll. J. Short, 22 February 1998. Photographed by J. Short. — 1 male, 9.5 × 6.2, 1 female (QM W17773), 6–9 m, 11.58.3 S 123.32.8 E, symbiotic with branching coral, *Acropora*, patch reef, SE side of reef, Hibernia Reef, Timor Sea, coll. 11 May 1992. — 1 male, 10.85 × 7.45 (QM W21603), 2–4 m, 27°29'S 153°25'E, symbiotic with *Acropora*, patch reef, Myora Reef, North Stradbroke Island, SE QLD, coll. QM party, 7 March 1996. — 1 ovigerous female, 11.1 × 7.2 (UF 18187), AUST-2102, AUST-ST-102MT, -14.4514° 145.3139°, rubble extraction, in dead *Pocillopora* head, Waining Reef, Lizard Island, coll. M. Timmers, 15 February 2009. — 1 male, 9.8 × 6.7 (UF 25981*), AUST-6668, HI09-101, 2–10 m, -23.4345° 151.9442°, Heron Island, coll. S. McKeon *et al.*, 25 November 2009. — 1 male, 10.5 × 7.2 (UF 25773*), Stn. HI09-101, -23.43447° 151.94423°, 2–10 m, Heron Island, Queensland, Australia, coll. S. McKeon *et al.*, 25 November 2009. — 1 male, 8.0 × 5.4 (UF 25636*), Stn. HI09-084, -23.45428333° 151.86711667°, Heron

Island, North Wistari, Queensland, Australia, coll. L. Avery *et al.*, 23 November 2009.

Philippines: 1 male, 7.5 × 5.0, 2 females, 1 juvenile (ZRC 2013.0681), Stn. B9, 8–10 m, 9°33.1'N 123°44.0'E, caves in the reef wall, Napaling, Panglao Island, coll. 8 June 2004. — 1 male, 10.25 × 6.80 (ZRC 2013.0682), Stn. B3, 8 m, 9°33.5'N 123°48.6'E, base of reef slope, Arco Point, Panglao Island, 31 May 2004. — 1 male, 8.60 × 5.60, 2 ovig. females (ZRC 2013.0683), B2, 5 m, 9°33.0'N 123°46.5'E, Alona Island, Panglao Island, coll. 31 May 2004. — 13 males, largest = 13.40 × 9.00, 8 females (ZRC 2013.0684), B22, 15–20 m, 9°29.4'N 123°56.0'E, rubble on mixed bottom, Pamilacan Island, coll. 24 June 2004. — 1 male, 9.50 × 6.40 (ZRC 2013.0685), B24, 38 m, 9°29.4'N 123°56.0'E, floor of cave, Pamilacan Island, 25 June 2004. — 1 male, 9.19 × 6.52, 1 ovigerous female, 11.7 × 7.8 (USNM 65177), shore, coral head, Marongas Islands, Philippine Expedition, Albatross, coll. 10 February 1908.

New Caledonia: 1 male, 10.9 × 7.1 (UF 37974*), NewC13-165, NEST6, 1–3 m, -22.6503° 167.387°, back reef to reef crest, Ile des Pins, New Caledonia, coll. N. Evans, 31 October 2013. — 1 male, 7.0 × 4.4 – 7.1 × 4.7 (UF 37970*), NewC13-293, NEST9, -22.6681° 167.425°, 1–2 m, rubble breaking, coral rubble, coralline algae, Ile des Pins, New Caledonia, coll. N. Evans, 2 November 2013.

Vanuatu: 3 males, 3.8 × 2.7 – 8.3 × 5.4, 6 females, 4.0 × 2.8 – 9.1 × 5.8, 7 juveniles (ZRC 2013.1606), Stn. DB53, 5 m, 15°28.8'S, 167°15.2'E, dead corals, Palikulo Bay, Vanuatu, coll. Santo Marine Biodiversity Survey, 22 September 2006. — 1 male, 6.8 × 4.5 (ZRC 2013.1607), Stn. DB46, 2–3 m, 15°28.8'S, 167°15.2'E, sandy flat, Palikulo Bay, Vanuatu, coll. Santo Marine Biodiversity Survey, 20 September 2006. — 7 males, 3.1 × 2.4 – 8.6 × 5.6, 3 females, 4.7 × 3.2 – 6.2 × 4.1, 2 ovigerous females, 6.1 × 4.0 – 6.3 ×

4.2, 3 juveniles (ZRC 2013.1608), Stn. FB52, 7 m, 15°42.7'S, 167°15.1'E, dead coral patches with algae, Malokilikili, Vanuatu, Santo Marine Biodiversity Survey, 05 October 2006.

Japan: 1 male, 5.9 × 4.0 (UF 26903*), GUOK10-2242, GUOK10-St-, 19 m, 24.4323° 123.7916°, fore reef, in coral rubble, Nakano Beach, Iriomote, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 9 July 2010. — 1 male, 7.7 × 5.0 (UF 26905), Stn. GUOK10-St-064, 24.432296° 123.791599°, 19 m, in coral rubble, fore reef, Iriomote, Nakano Beach, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 9 July 2010. — 1 male, 12.0 × 7.8 (UF 28678), Stn. FMOK11-St-36, 26.695479° 128.018979°, 1–2 m, on immersed cages in harbor, harbor, Kouri Island harbor, Okinawa, Ryukyus, Japan, coll. F. Michonneau, 21 May 2011.

Caroline Islands: 1 male, 7.3 × 5.1 (USNM 1191879), Ifaluk, coll. Abott, 1953, Acc. No. 200652, 99-D. — 1 ovigerous female, 9.0 × 6.2 (UF 3908), Stn. BPAL-108, 7.26648333° 134.4732333°, 26 m, on Inner side of Sunken Barrier Reef About 1km Off of Lighthouse Channel (=toachal Ra Kesebekuu), Pat Colins "*Goniopora* Flats", Palau, coll. G. Paulay, 9 March 2003.

Marshall Islands: 1 male, 7.4 × 5.0 (USNM 1191869), dredged in lagoon, Bikini Atoll, coll. K. Emory, April 1946, S-46-109, Acc. No. 172 586. — 1 male, 10.1 × 7.9 (USNM 1191858), 180-200 ft, Bikini Lagoon, coll. L. Schultz, 29 March 1946, Acc. 172 586. — 1 male, 6.0 × 4.1, 1 female, 7.2 × 4.9 (USNM 1191878), on anchor in lagoon, Rongelap Island, coll. M. Johnson, 1 June 1946, Acc. No. 172586.

Diagnosis. Carapace (Pl. 15B) transversely hexagonal, ca. 1.5 broad as long, dorsal surface minutely to moderately granular, appearing smooth without magnification, anterolateral regions defined, 2L, 3L, 4L distinctly raised, 1–3M poorly defined, with distinct longitudinal depressed medial line from front to anterior margin of 3M, posterior border of 3M with slight H-shaped groove, usually with tufts or scattered setae on anterolateral borders of 2M and 5L, sometimes more scattered on anterior or anterolateral regions. Front (Pl. 15C) broad, double rimmed, lobes sinuous, separated by V-shaped notch. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low, obtuse; teeth 2–4 larger, anteriorly directed, often spine tipped, tooth 4 with transverse granular crest marking posterior border of 4L. Anterolateral angle of basal antennal segment produced, reaching halfway or more into orbital hiatus. Pterygostomial region usually with no or few plumose setae mesially, becoming more dense laterally. Chelipeds (Pl. 15E, F) unequal, tips of fingers hollowed, spoon-like; outer surface of chelae smooth. Ambulatory legs (Pl. 15A) with numerous long plumose setae, scattered long simple setae, row of short spines on extensor margins; tip of dactylus bifid; distal pigmented spine sub-equal to curved tip. Male thoracic sternum (Pl. 15D) with press button located on sternite 5, 3/4 way to suture between sternites 4, 5. Male abdomen (Pl. 15D) long; somites 3 to 5 fused, sutures not discernible; somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 39D) convex, bent 3/4 way to tip; apex pointed, spatulate, longitudinally hollowed, with row of subdistal setae and short spines.

Remarks. This species can be distinguished from its congeners in having a granular carapace, especially evident on anterolateral regions, (usually) tufts of setae on the anterolateral margins of the carapace regions 2M and 5L, and anterolateral regions marked by elevations (Pl. 15B) (vs. without tufts of setae in all *Chlorodiella species*). It is closest in external morphology to *Chl. nigra* and in gonopod morphology to *Chl. ohshimai* (see remarks of these two species). *Chlorodiella xishaensis* inhabits live coral, dead coral rubble, or rocks in coral reef areas.

Distribution. *Chlorodiella xishaensis* is recorded from the Parcel (Xisha) Islands and Okinawa, Japan, throughout the Philippines and into the Great Barrier Reef—i.e., the coral triangle and adjacent areas (Pl. 48B). It is recorded from Vanuatu here for the first time. Serène (1984: pl. XLIII F) recorded one female specimen from Madagascar, while stating that although the specimen is more spinose (likely referring to the anterolateral teeth) than conspecifics he had examined from the Philippines and Xisha, it is likely *Chl. xishaensis*. However, the sharp and anteriorly directed anterolateral teeth, as well as the carapace regions, indicate that this specimen is probably a young *Chl. nigra*.

Cyclodius Dana, 1851

Cyclodius Dana 1851: 126. — Ng *et al.* 2008: 197.

Chlorodius (*Phymodius*) A. Milne-Edwards 1863: 263.

Phymodius, A. Milne-Edwards 1873: 217. — Alcock 1898: 161. — Stebbing 1910: 299. — Sakai 1939: 509; 1976: 463. — Barnard 1950: 215. — Forest & Guinot 1961: 104. — Guinot 1964b: 71. — McNeill 1968: 61. — Serène 1984: 245. — Dai, Yang, Song, & Chen 1986: 309. — Dai & Yang 1991: 333.

Key to the Species of *Cyclodius*.

1. Carapace and external surfaces of chelipeds covered in short, light-colored setae..*Cyc. paumotensis*
– Carapace and external surfaces of chelipeds with few or no setae...2

2. Frontal submedian lobes separated by wide, deep, V-shaped notch (Pl. 18B)..*Cyc. granulosus*

– Frontal submedian lobes separated by shallow V- or U-shaped notch..3

3. Carapace region 2M longitudinally divided by distinct, deep furrow.....4

– Carapace region 2M not divided or indistinctly divided.........................6

4. Carapace surface coarsely but strongly granulate. G1 with numerous long, distally-directed setae...5

– Carapace surface appearing smooth without magnification or covered with relatively small granules. G1 with numerous long, proximally-directed setae (Pl. 41D)...*Cyc. ungulatus*

5. Carapace relatively broad (W/L ≥ 1.5)..................................*Cyc. drachi*

– Carapace relatively narrow (W/L < 1.5).........................*Cyc. granulatus*

6. Carapace relatively flat, glossy. Regions relatively flat, medially separated by narrow furrows. Posterolateral margin longer than anterolateral region. G1 with numerous long, distally-directed subdistal setae..*Cyc. nitidus*

– Carapace convex. Medial region markedly convex, regions separated by broad furrows. Posterolateral margin roughly equal to anterolateral margin. G1 with numerous short, stout, proximally-directed setae or spines (Pl. 41A)...*Cyc. obscurus*

Cyclodius drachi (Guinot, 1964)

Pls (16, 40A)

Phymodius drachi Guinot 1964b [type locality = Madagascar; Nosy Be, Madagascar; Red Sea]: 72, figs 42, 47, pl. 3, fig. 1, pl. 7, fig. 1; 1967c: 267 [List]. — Serène 1968: 81 [List]; 1984: 249–250, fig. 154, pl. XXXV D [NE Coast of Madagascar, Nosy Be, Madagascar; Mombasa, Kenya; Mayotte, Comoros]. — ?Dai, Yang, Song & Chen 1986: 313, pl. 45(2), fig. 167B [Review]. — Dai & Yang 1991: 313, pl. 45(2), fig. 167B [Review].

Phymodius ungulatus, Nobili 1906c: 264 [Red Sea]. [not *Cylodius ungulatus* (H. Milne Edwards, 1834)].

Material examined. *Madagascar:* holotype male, 15.9 × 10.6 (MNHN-B13117), Madagascar, coll. Millot.

Diagnosis. Carapace (Pl. 16B) transversely hexagonal, ca. 1.5 times broad as long; dorsal surface granulate, punctate; regions separated by deep furrows; 2M longitudinally divided; 3M faintly tripartite. Front (Pl. 16C) broad; submedian lobes convex, joining medially to form U-shaped notch, separated from projecting lateral lobes by concavity. Anterolateral margin with 4 lobular teeth excluding outer supraorbital tooth; tooth 1 relatively narrow; teeth 2, 3 large, ca. equal in size; tooth 4 relatively small. Anterolateral angle of basal antennal segment not produced, flagellum free to enter orbit. Pterygostomial region granulate with plumose setae diagonally from posterior to lateral surface. Chelipeds (Pl. 16E, F) subequal, stout, external surfaces covered in large granulate protuberances; anterior margin of merus lined with large conical or blunt granules; fixed finger with black pigment extending almost 1/2 length of lower margin and into external surface. Ambulatory legs (Pl. 16A) stout, granulate, covered with long, plumose setae, especially on extensor surface; extensor margin lined with sharp, arched spines; tip of dactylus with single distal, pigmented spine and usually two smaller, downward-pointing, subdistal spines. Male thoracic sternum (Pl. 16D) minutely granulate, with posterior setae. Male abdomen (Pl. 16D) relatively broad; somite 6 approximately as broad as long, anterior margin broader than posterior; telson ca. as broad as long. G1 (Pl. 40A) relatively stout, laterally compressed; with short spines, more than 20 long, plumose, subdistal setae; apex spatulate, longitudinally hollowed, relatively wide.

Remarks. In her description of *Cyclodius drachi*, Guinot (1964: 72) made thorough comparisons with *Cyc. ungulatus*, *Cyc. granulatus*, and *Cyc. nitidus*. The differences in G1 morphology highlighted between *Cyc. drachi, Cyc. ungulatus*, and *Cyc. nitidus* are quite clear (Pls 40A, D, 41D). On the contrary, examination of the holotypes of *Cyc. granulatus* and *Cyc. drachi* has revealed that these species are very similar, or possibly conspecific. Most notably, the G1s are almost indistinguishable (Pl. 40A, B). Guinot (1964) stated that they are similar, but differ in the apical lobe and ornamentation of setae. However, her figures do not illustrate these differences. Furthermore, the holotype G1 only differs in apical lobe morphology. That of *Cyc. drachi* is slightly wider, but this may amount to intraspecific variation. The most distinct differences between these species are the granulation of the carapace and chelae, and relative width of the carapace (Pls 16B, 17B). The holotype of *Cyc. drachi* looks as if the granulation has worn, possibly due to abrasion. The relative width of the carapace, however, is distinctly greater. Whether the relative width of this species is related to age and/or size will require the examination of more specimens of different sizes. Unfortunately, both species are relatively rare and a large serious of specimens was not available for examination.

Distribution. *Cyclodius drachi* is only known from the Red Sea and western Indian Ocean (Pl. 48C).

Cyclodius granulatus (Targioni-Tozzetti, 1877)

Pls (17, 40B, 48D)

Pilodius granulatus Targioni-Tozzetti 1877: 50, pl. 4, fig. 15-19, 20-21, 24a [Red Sea].

Chlorodopsis inoequalis Klunzinger 1913: 227 [Red Sea].

Phymodius granulatus Nobili 1905c: 490 [Key]; 1906c: 265 [Djibouti; Red Sea]. — Klunzinger 1913: 227 (131), pl. 3, fig. 3 [Red Sea]. — Balss 1924a: 10 [Lidth(?), Red Sea]. — Gordon 1934: 41, fig. 19b, 20b, 21b [Bay of Djibouti; Suez Canal, Gulf of Suez; Daedalus Shoal, Red Sea; Egypt; Sudan]. — Ramadan 1936: 33 [Ghardaqa, Egypt, Red Sea]. — Monod 1938: 127 [Bay of Suez]. — Stephensen 1946: 157, fig. 38 [Kharg I. and Bushire, Iranian Gulf]. — Forest & Guinot 1961: 113, pl. 16, fig. 1-3 [Obock, Djibouti]. — Guinot 1962b: 238 [Sarso Island, Saudi Arabia]; 1964a: 12 [Red Sea; Xaafuun, Somolia]; 1964b: 82, fig. 44, 48, pl. 7, fig. 2 [Abulat, Saudi Arabia]; 1967c: 267 [List]. — Serène 1968: 81 [List]; 1984: 250, fig. 155, 159, pl. XXXV B [Ambouli Reef, Red Sea]. — Serène *et al*. 1976: 18 [List].

Cyclodius granulatus Davie 2002: 521 [List].

Chlorodopsis arabica Laurie 1915: 450, pl. 42, fig. 1-1 b, pl. 43, fig. 2, 4 a-d [Sudan, Red Sea]. — Calman 1927: 213 [Gulf of Suez].

Chlorodius dehaani Heller 1861c, 337 [Red Sea].

Pilodius spinipes, Serène 1984: 243 (part). [not *Luniella spinipes* (Heller, 1861)]

Material examined. *Red Sea:* 1 male, 16.4 × 11.2 (UF 36780*), Stn. SAFA-014, 18.19168° 41.1138°, 9–11 m, sandy shoal with patch reefs, Farasan Banks, Atlantis Shoal, Saudi Arabia, coll. A. Anker *et al*., 7 March 2013.

Saudi Arabia: 1 male, 8.1 × 5.7 (UF 37172*), Stn. SAFA-039, 20.167155° 40.223307°, 1–2 m, mangroves, Al Lith, Saudi Arabia, coll. A. Anker *et al*., 21 March 2013. — (?) 1 female, 8.7 × 5.9 (UF 36907), Stn. SAFA-018, 16.75273° 41.60488°, 1–5 m, silty reef flat to slope, Farasan Islands, Naf Shuma, Saudi Arabia, coll. A. Anker *et al*., 9 March 2013.

Djibouti: 1 male, 14.2 × 9.9, 1 female, 7.3 × 5.2 (UF 33095*), BDJRS-1267, DJRS-002, 7–17 m, 11.6992° 43.1432°, reef slope, Sunken Buoy dive site, Maskali Bank, Moucha Islands, Djibouti, 27 September 2012. — 4 females, 13.4 × 9.3 – 4.7 × 3.6 (UF 37892*), BDJRS-0190, DJRS-007, 8–13 m, 11.976° 43.365°, in dead coral, reef slope, E of Obock, NE Gulf of Tadjoura, Djibouti, coll. G. Paulay, 29 September 2012. — 1 male, 16.1 × 11.2, 1 female, 12.3 × 8.5 (MNHN B6776), Ambouli Reef, Djibouti, coll. Dantan, 30 March 1933.

Persian Gulf: 4 males, 7.2 × 5.0 – 11.75 × 7.94, 3 females, 6.1 × 4.2 – 9.8 × 7.7, 1 juvenile, 3.7 × 2.8 (USNM 93953), Stn. HO-7, Persian Gulf, Arabian Sea, coll. Hydrographic Office.

Diagnosis. Carapace (Pl. 17B) transversely hexagonal, ca. 1.4 times broad as long; dorsal surface convex, strongly granulate; regions separated by deep furrows; 2M longitudinally divided; 3M entire or faintly tripartite. Front (Pl. 17C) broad; submedian lobes convex, joining medially to form deep U-shaped notch, separated from projecting lateral lobes by concavity. Anterolateral margin with 4 lobular teeth excluding outer supraorbital tooth; tooth 1 relatively narrow; teeth 2, 3 large ca. equal in size, subtriangular, sometimes tipped with conical granule; tooth 4 relatively small, sometimes tipped with short spine. Anterolateral angle of basal antennal segment entering less than halfway into orbital hiatus, flagellum free to enter orbit. Pterygostomial region granulate. Chelipeds (Pl. 17 E, F) unequal to subequal, stout, external surfaces covered in large granulate protuberances; anterior margin of merus lined with short spines or conical granules; fixed finger with black pigment extending almost 1/2 length of lower margin and onto external surface. Ambulatory legs (Pl. 17A) stout, granulate, covered with long, plumose setae, especially on extensor surface; extensor margin lined with sharp, arched spines; tip of dactylus with single terminal, pigmented spine and usually two smaller, downward-pointing, subdistal spines. Male thoracic sternum (Pl. 17D) minutely granulate, with posterior setae. Male abdomen relatively (Pl. 17D) broad; somite 6 ca. broad as long, anterior margin broader than posterior; telson ca. broad as long. G1 (Pl. 40B) relatively stout, laterally compressed; with > 20 long, plumose subdistal setae, short spines; apex spatulate, longitudinally hollowed, relatively wide.

Remarks. This species is distinguished from *Cyc. drachi* by its strong granulation of the carapace and chelae, relatively narrow carapace, and G1 morphology (but see Remarks for *Cyclodius drachi*). These features are similar to *Cyc. granulosus* (Pl. 18A, B, 40C). Both species have granulate, narrow carapaces and similar G1s possessing long, subdistal setae and a spatulate apex with a rounded distal margin. However, *Cyc. granulatus* has a front with mesial lobes separated by a U-shaped notch and more numerous, long subdistal setae on its G1 [versus gaping V-shaped notch and less setae in *Cyc. granulosus* (Pl. 18B, 40C)].

It is very difficult to differentiate between young members of this species and those of *Cyc. ungulatus* (see Guinot 1964). Adult *Cyc. ungulatus* specimens usually have a much smoother carapace, although granulation is not uncommon. However, besides the very different G1s, the setation of the ambulatory legs is useful for differentiating between the two species. *Cyclodius granulatus* has ambulatory legs that are covered in long, thick, plumose setae (Pl. 17A) [versus less dense, shorter plumose and simple setae in *Cyc. ungulatus* (Pl. 23A)].

Distribution. *Cyclodius granulatus* has only been recorded from the Red Sea, Gulf of Aden, and Persian Gulf (Pl. 48D).

Cyclodius granulosus De Man, 1888

Pls (18, 40C, 49A)

Cyclodius granulosus De Man 1888b: 283, pl. 11, fig. 1 [Ambon Island, Indonesia]. — Davie 2002: 521 [List]. — Ng *et al*. 2008: 197.

Phymodius sp. Gordon 1934: 43, fig. 19 d [Banda Neira, Indonesia].

Phymodius granulosus Guinot 1964b: 76, figs 39-41, 46, 49 a, b, pl. 3**,** fig. 2, pl. 9, fig. 1-2 [Diego Suarez, Madagascar]; 1967c: 267 [list]. — Sakai 1967: 82; 1976: 463, pl. 165, fig. 3 [Yoron I., Ishigaki I., and Taketomi I., Japan]. — Serène 1968: 81 [List]; 1984: 252, fig. 162, 163, pl. 35 F [no new collections]. — Dai *et al.* 1986: 310, pl. 44(4) [Review]. — Dai & Yang 1991: 334, pl. 44(4) [Review].

Phymodius ornatus, Sakai 1939: 509, fig. 45 [Loo Choo, Japan]. (not *Cyclodius ornatus* Dana, 1852)

Material examined. *Saudi Arabia:* (?)1 juvenile (UF 37005), Stn. SAFA-025, 16.83585° 42.30625°, 2–6 m, in rubble, fringing reef/slope around sand cay, Farasan Islands, Zahrat Durakah, Saudi Arabia, coll. A. Anker *et al*., 11 March 2013.

Scattered Islands: 2 females, 8.3 × 6.4 – 11.3 × 8.4 (UF 21190*), Stn. GLOR-2, -11.59088333° 47.2851333°, 7–14 m, reef platform and shallow canyons, Iles Eparses, Glorieuses, Glorieuses Island, Scattered Islands, France, coll. H. Bruggemann *et al.*, 4 May 2009.

Chagos: 2 males (larger = 16.05 × 11.30), 1 female, 1 juvenile (ZRC 2013.0779), CH0562, 10m approx., dead branching coral heads, outer reef, Peros Banhos, Chagos Archipelago, coll. C. Head & H. Koldeway, 25 February 2013. — 1 ovigerous female, 16.30 × 11.80 (ZRC 2013.0784), CH0831, 10m approx., dead branching coral heads, outer reef, Diego Garcia, Chagos Archipelago, coll. C. Head & H. Koldeway, 3 March 2013. — 1 male, 13.90 × 10.05, 1 juvenile (ZRC 2013.0775), CH0838, 10m approx., dead branching coral heads, outer reef, Diego Garcia, Chagos Archipelago, coll. C. Head & H. Koldeway, 4 March 2013. — 1 male, 13.50 × 10.00 (ZRC 2013.0778), CH0877, 10m approx., dead branching coral heads, outer reef, Diego Garcia, Chagos Archipelago, coll. C. Head & H. Koldeway, 5 March 2013.

Philippines: 1 female, 8.3 × 6.2 (ZRC 2008.0649), dive resort environs, Balicasag Island, Philippines, coll. H. Tan, 26–27 July 2003.

Mariana Islands: 1 juvenile, 4.4 × 3.4 (USNM 1184684), Stn. GUM 053, ca. 300 m N of boat basin channel, Agana Bay, Guam, coll. R. Kropp, 3 February 1984. — 1 female, 10.9 × 8.0 (UF 1248*), Stn. ZZZ-085731, 13.5° 144.8°, 10–20 m, among rocks, Apra Harbor, Glass Breakwater, near harbor entrance, Guam Island, Mariana Islands, USA, coll. H. Conley, 22 August 1984. — 1 male, 7.9 × 6.0 (UF 3017*), 25 m, Apra Harbor, Glass Breakwater, near harbor entrance, Guam Island, Mariana Islands, coll. H. Conley, 18 May 2002.

Line Islands: 1 juvenile, 4.8 × 3.8 (UF 11177*), MSR-157-DP, KINF16-DP, 40 ft, 6.3796° -162.3648, outer reef slope, dead *Pocillopora verrucosa?*, S shore of Atoll, Kingman Reef, Line Islands, coll. 28 August 2005. — 1 male, 7.9 × 5.3 (UF 10499*), BPALM-811, GP-Loc-848, 9–15 m, 5.8693° -162.0757°, outer reef slope, from dead *Pocillopora ?verrucosa* head, SSW side of atoll, Palmyra Atoll, Line Islands, coll. G. Paulay & N. Knowlton, 18 August 2005. — 1 male, 5.2 × 4.1 (UF 11110*), Stn. PALB4-DP, 5.8958 -162.0815, 35- m, dead *Pocillopora verrucosa*? head, outer reef slope, N side of Atoll, Palmyra Atoll, Line Islands, USA, coll. N. Knowlton & G. Paulay, 19 August 2005.

Diagnosis. Carapace (Pl. 18B) hexagonal, ca. 1.4 times broad as long; dorsal surface granulate, with few tufts of plumose setae; regions well defined; 2M completely or partially longitudinally divided; 3M entire; anterior border of 2M, 5L with tuft of plumose setae. Front (Pl. 18C) broad; submedian lobes advanced, oblique, relatively straight, margins granulate, joining medially to form broad, deep V-shaped notch; lateral lobes narrow, projecting. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 small, acute, anteriorly directed, ventrally located; teeth 2, 3, 4 approximately equal in size, acute, anteriorly directed, sharp. Anterolateral angle of basal antennal segment entering less than halfway into orbital hiatus, flagellum free to enter orbit. Pterygostomial region granulate. Third maxilliped exopod with distal tuft of plumose setae. Chelipeds (Pl. 18 E, F) subequal, external surfaces spinose; anterior margin of merus with one or few long spines; pigmentation restricted to fixed finger. Ambulatory legs (Pl. 18A) stout, granulate, covered with long, plumose and/or simple setae; extensor margin lined with sharp, arched spines; tip of dactylus bifid, pigmented spine longer than downward-pointing, subdistal spine. Male thoracic sternum (Pl. 18D) granulate. Male abdomen (Pl. 18D) long; somite 6 ca. broad as long; telson longer than broad. G1 (Pl. 40C) moderately stout; with ca. 10 long, simple subdistal setae, short spines; apex spatulate, longitudinally hollowed, tip rounded.

Remarks. Guinot (1964) reviewed the puzzling taxonomy of *Cyclodius granulosus* and included a figure of De Man's (1888) young holotype (9.3 × 6.2), noting that the type is not male, but female, in contrast with what is stated in the original description. She also synonymized Gordon's (1934) "*Phymodius* sp?" specimen with *Cyc. granulosus*. According to Guinot (1964), a key diagnostic feature of the species is the gaping V-shaped notch of the front, a feature which is not present in the holotype, but present in Gordon's undetermined specimen. Guinot examined a series of various sized specimens and concluded that a deep V-shaped notch of the front is not always present in young specimens. However, Serène (1984) questioned whether some of the young specimens Guinot (1964) examined—5 juveniles from Madagascar identified by Balss as *Chlorodopsis* aff. *scabricula*—were, in fact, *Cyc. ungulatus* and not *Cyc. granulosus*. If they were not *Cyc. granulosus* specimens, the identity of the *Cyc. granulosus* holotype is uncertain.

Several additional young specimens (UF 11177, UF 10499, UF 3017, and USNM 1184684) that are smaller than the holotype were examined. All of these have the diagnostic pronounced, wide V-shaped notches on the front. Additionally, the holotype specimen is quite similar to juvenile *Cyc. ungulatus*. Given the ambiguous nature of the historical material and observations for this study, the validity of *Cyc. granulosus* is in doubt, and it may be a junior synonym of *Cyc. ungulatus*. In this case, the "V-shaped notch" species would be new. However, examination of the holotype, the questionable Malagasy material, and a larger series of juvenile and adult specimens are necessary before giving the species a new name.

Guinot (1964) provided several features to aid in distinguishing between *Cyc. granulosus* and *Cyc. ungulatus*, beyond the morphology of the front. According to her, *Cyc. granulosus* has: 1) projecting rows of granules and light-colored tufts of setae on the carapace (versus absent in *Cyc. ungulatus*); 2) major and minor chelae relatively similar in size and shape (versus markedly unequal in *Cyc. ungulatus*); 3) more developed spination of the ambulatory legs (versus less developed in *Cyc. ungulatus*); and 4) a G1 with ca. 10 simple, subdistal setae (versus numerous stout proximally directed setae in *Cyc. ungulatus*). The gaping V-shaped notch of the front and G1 morphology are the best characters for differentiating between these species, and the remaining *Cyclodius* species, as the other characters may vary with age. However, these other features can be used with care when large adult specimens are not available.

Cyclodius granulatus and *Cyc. drachi* are also similar to *Cyc. granulosus*, especially young specimens. The male gonopods of these two species, however, are much stouter and bear numerous plumose subdistal setae (Pls 40A, B) [versus narrow with less and simple setae in *Cyc. granulosus* (Pl. 40C)]. Furthermore, the presence of the V-shaped notch and relatively few setae on the ambulatory legs are useful features as well (Pl. 18A, B); *Cyc. granulatus* and *Cyc. drachi* have fronts with a shallow notch and legs with numerous, plumose setae (Pls 16A, B, 17A, B). The carapace of *Cyc. granulosus* is also relatively narrower than *Cyc. drachi.*

In comparison with *Cyc. nitidus* and *Cyc. sculptus*, *Cyc. granulosus* has a much narrower, more granulate carapace, with region 2M divided longitudinally (Pl. 18B) [versus wider, smooth and entire 2M in *Cyc. sculptus* and *Cyc. nitidus* (Pls 19B, 22B)]. The gonopods of these species are similar, but that of *Cyc. granulosus* has less and narrower subdistal setae and a slightly more open distal lobe (Pl. 40C) [versus generally more numerous, stouter setae and more folded apex in *Cyc. nitidus* and *Cyc. sculptus* (Pls 40D, 41C)]. *Cyclodius granulosus* is easily distinguished from *Cyc. obscurus* in having a relatively flatter, granulate carapace and deep, wide V-shaped notch of the front (Pl. 18B) [versus smooth, strongly concave carapace and shallow V-shaped notch in *Cyc. obscurus* (Pl. 20B).

Distribution. Serène (1984) questioned whether several Malagasy specimens identified by Guinot (1964) were correctly identified, casting doubt on the species' presence in the Western Indian Ocean. The identity of those specimens remains uncertain. However, specimens were examined from the Red Sea and Scattered Islands with the diagnostic V-shaped front (see remarks). The distribution of this species is widespread, from the Western Indian Ocean to the Line Islands (Pl. 49A).

Cyclodius nitidus (Dana, 1852)

Pls (19, 40D, 53B)

Pilodius nitidus Dana 1852: 80 [Tutuila, American Samoa]; 1852b: 218 [Tutuila Island, Samoa]; 1855: pl. 12, fig. 7 a–e [Atlas]. — Nobili 1907: 393 [Kaukura, Tuamotus].

Phymodius nitidus, Rathbun 1906: 858 [Honolulu, Waikiki, and Molokai, Hawaii]; 1911: 225 [Praslin and Coetivy, Seychelles]. — Edmondson 1923a: 17 [Palmyra I.; Fanning I.]; 1925: 44 [Pearl and Hermes Reef, French Frigate Shoals, Lisiansky I., Necker, Johnston, and Wake, Hawaiian Is.]; 1933: 250, fig. 152 c [Review]; 1962: 280 [Hawaiian Is.]. — Gordon 1934: 39, fig. 20 a, 21 a [Seychelles; Daidalus Shoal, Red Sea; Galle, Sri Lanka; Christmas I., Pukoo, Molokai, Hawaiian Is.]. — Balss 1938a: 55–56 [Aranuka, Gilbert

Islands]. — Holthuis 1953: 24 [Saipan, Mariana Islands]. — Forest & Guinot 1961: 114, pl. 15, fig. 1–4 [Tahiti]. — Guinot 1962b: 238 [Addu Atoll, Maldives]; 1964b: 84, fig. 43, 50, pl. 8, fig. 1 [Abulat, Saudi Arabia]; 1967c: 267 [List]. — Sakai 1967: 81; 1976: 464, pl. 165, fig. 2 [Yoron I., Ishigaki I., and Taketomi I., Japan]. — Serène 1968: 81 [List]; 1984: 249, fig. 153, pl. XXXV [Nosy Iranja, Nosy Be and Fort-Dauphin, Madagascar; Iles Glorieuses; Mombasa, Kenya]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]; 1989: 113 [Tikehau, Tuamotu]. — Dai *et al*. 1986: 310, pl. 43(3), fig. 167A(1) [Review]. — Dai & Yang 1991: 333, pl. 43(3), fig. 167A(1) [Review]. — DeFelice *et al*. 1998: 16 [Midway Atoll, Hawaiian Is.]. — Coles *et al*. 2001: 54 [List]. — DeFelice *et al.* 2002: 30, 72 [French Frigate Shoals, Hawaiian Is.]. — Coles *et al*. 2002a: 271, 334 [Oahu, Hawaii]. — Coles *et al*. 2002b: 194, [Oahu, Hawaii].

Cyclodius nitidus Davie 2002: 522 [List]. — Ng *et al*. 2008: 197 [List].

Chlorodius sculptus A. Milne-Edwards 1873a: 217, pl. 8, fig. 4 [Seychelles, Samoa, New Caledonia]. — De Man 1881: 98; 1887: 32; 1887b: 279 [Noordwachter Island, Indonesia]. — Ortmann 1893: 466 [Samoan Is.].

Phymodius sculptus Alcock 1898: 164 [Andaman Islands, India; Sri Lanka; Mergui Archipelago, Myanmar]. — Calman 1900: 12 [Torres Straits]; 1909: 705 [Christmas Island]. — Borradaile 1902: 259 [Male, Goifurfehendu, Maldives]. — Nobili 1905c: 490 [Key]; 1906c: 265 [Red Sea]. — Lenz 1905: 354 [Zanzibar, Tanzania; Kokotoni, Kenya]; 1910: 550 [St. Mary and SW, Madagascar]. — Grant & McCulloch 1906: 13 [Mast Head I., Australia]. — Laurie 1906: 405 [Galle, Sri Lanka]; 1915: 450 [Sudan, Red Sea]. — Rathbun 1911: 225 [Salomon, Praslin]. — Klunzinger 1913: 221 (125), pl. 6, fig. 11 [Red Sea]. — Laurie 1915: 450 [Sudan, Red Sea]. — Balss 1924a: 10 [Koseir, Haleib, Lidth, Zebejir?, St. Johns I?]. — Ward 1932: 250 [One tree I., Australia]. — Ramadan 1936:

33 [Ghardaqa, Egypt, Red Sea]. — Sankarankutty 1962: 137, figs 36, 37 [Nicobar I.].

Chlorodopsis scabricula, Rathbun 1906: 859 [Hawaiian Islands]; 1907: 50, pl. 1, fig. 3, pl. 9, fig. 5 [Papeete, Tahiti]. — Serène & Luom 1959: 318 [Review]. (not *Pilodius scabriculus* Dana, 1852)

Material examined. *Saudi Arabia:* 1 female, 19.3 × 12.4 (UF 36521), Stn. SAFA-005, 19.00533° 40.14815°, 1–7 m, in *Tubipora* rubble, reef lagoon and barrier reef flat, offshore of Farasan Banks, Dolphen Lagoon, Saudi Arabia, coll. A. Anker *et al.*, 4 March 2013. — 2 males, 7.8 × 5.2 – 18.6 × 12.2, 1 female, 16.3 × 10.5 (UF 33025 – 33026*), Stn. DJRS-035, 22.26455° 39.0263°, 1–20 m, seaward reef slope & front of shelf reef, Thuwal, Abu Gishaa, Saudi Arabia, coll. G. Paulay, 8 October 2012.

Djibouti: 1 female, 20.2 × 12.8 (UF 32927*), Stn. DJRS-019, 11.55875° 42.74083°, 1–15 m, reef slope, SW Gulf of Tadjoura, Outside Bay de Ghoubbet, Stony Cove, Djibouti, coll. G. Paulay, 2 October 2012.

Seychelles: 1 male, 11.3 × 7.4, 1 female, 15.9 × 10.1 (USNM 41259), Praslin Island, Seychelles, Indian Ocean, coll. Sealark Expedition, Sealark R/V, 1905. — 1 male, 12.3 × 8.4, 1 female, 12.0 × 7.9 (USNM 41257), Coetivy Island, Seychelles, Indian Ocean, coll. J. Gardner, Sealark Expedition, Sealark R/V, 1905.

Christmas Island: 1 male, 9.8 × 6.5 (ZRC 2013.1630*), Stn. CI-D03-2011 (093), 3-27.5 m, S10° 27.805', E105° 42.443', shore dive, reef slope, rubble beds, Ethel Beach, coll. Christmas Island Expedition, H. Tan *et al.*, 24 March 2011. — (?) 4 males, 14.8 × 9.5 – 20.3 × 12.4, 2 females, 13.7 × 8.9 – 16.7 × 10.2 (ZRC 1965.11.11.10–15), Christmas Island.

Australia: 1 male, 18.0 × 11.3 (UF 17031*), AUST-1038, AUST-ST-041, 2–3 m, hand, dip net, under rocks and in rubble, rubble on sand, corals, back reef flat, first snorkelling site, Waining Reef, coll. A. Anker & R. Lasley, 15 February 2009. — 1 female, 7.2 × 4.9 (UF 24858*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 female, 12.3 × 8.1 (UF 25559*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009. — 1 female, 6.4 × 4.2 (UF 24806*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 female, 13.3 × 8.7 (UF 16656*), Stn. AUST-ST-004, -14.6928° 145.4668°, 1–2 m, under rocks, rubble, reef flat, Lizard Island, off Bird Island, Queensland, Australia, coll. A. Anker & R. Lasley, 8 February 2009. — 1 male, 12.3 × 8.0 (UF 17128), ?Lizard Island, 2009. — 1 male, 7.4 × 5.0 (UF 25633*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll., 23 November 2009. — 1 male, 10.1 × 6.7 (UF 24884*), Stn. HI09-019, -23.43135° 152.03375°, 1–2 m, under rock, reef crest, reef flat, Heron Island, Sykes Reef, Queensland, Australia, coll. F. Michonneau & R. Lasley, 14 November 2009. — 1 female, 10.8 × 7.0 (UF 17175*), Stn. AUST-ST-059, -14.7468° 145.5163°, 2 m, under rocks, coral, fore reef, Lizard Island, near Northern Direction Island, Queensland, Australia, coll. R. Lasley, 19 February 2009. — 1 male, 20.8 × 12.4 (UF 24787*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 male, 18.1 × 11.4 (UF 24789*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 male, 17.0 × 10.3 (UF 16638*), Stn. AUST-ST-004, -14.6928° 145.4668°, 1–2 m, under rocks, rubble, reef flat, Lizard Island, off Bird Island, Queensland, Australia, coll. A. Anker & R. Lasley, 8 February

2009. — 23.5 × 14.8 (UF 24786*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009. — 1 female, 18.4 × 11.9 (UF 16657*), Stn. AUST-ST-004, -14.6928° 145.4668°, 1–2 m, under rocks, rubble, reef flat, Lizard Island, off Bird Island, Queensland, Australia, coll. A. Anker & R. Lasley, 8 February 2009.

Indonesia: 1 male, 12.2 × 8.0, 1 female, 11.3 × 7.4 (USNM 154927), Lembek Strait, Celebes Island, Greater Sunda Islands, Sulawesi, Indonesia, coll. A. Herre.

Japan: 1 male, 10.7 × 7.0 (UF 28660*), Stn. FMOK11-St-22, 26.251732° 127.672239°, 0–1 m, in rubble, artificially sheltered fringing reef, Inamuse, Okinawa, Ryukyus, Japan, coll. F. Michonneau & Y. Ryuta, 15 May 2011. — 1 juvenile (UF 28666*), Stn. FMOK11-St-22, 26.251732° 127.672239°, 0–1 m, in rubble, artificially sheltered fringing reef, Inamuse, Okinawa, Ryukyus, Japan, coll. F. Michonneau & Y. Ryuta, 15 May 2011.

Caroline Islands: 1 female, 16.5 × 10.5 (USNM 154928), 7 13 9 N 134 26 40 E, Ngaremediu reef flat, Palau, coll. F. Bayer, 19 August 1955. — 1 female, 11.3 × 7.3 (USNM 106578), Stn. 33-B, intertidal, reef E of S end of island, Falarik Island, Ifalik Atoll, Yap Islands, Caroline Islands, Micronesia, coll. D. Abbott, 4 September 1953.

Mariana Islands: 1 male, 12.4 × 8.0 (UF 4074*), Stn. GP-Loc-752, 13.4245333° 144.7858167°, 0–1 m, on and under rocks, outer reef flat, N Pago Bay, Guam Island, Mariana Islands, USA, coll. G. Paulay, May 2003. — 1 female, 17.6 × 11.0 (UF 710*), Stn. BGUAM-086, 13.5° 144.8°, 2 m, deep in rubble, outer reef flat, Urunao Reef, S Side, Guam Island, Mariana Islands, USA, coll. G. Paulay & G. Meyer, 1 June 2000. — 1 male, 11.8 × 7.8 (UF 74), Stn. HTC-0001, 13.5° 144.8°, 5 m, deep in coral rubble, fore reef, Agat Bay, N of Alutom Islet, Guam Island, Mariana Islands, USA, coll. H. Conley, 15

November 2000. — (?) 1 female, 19.2 × 11.8, 1 ovigerous female, 18.0 × 10.9 (USNM 154930), coral heads, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945. — (?) 2 males, 7.2 × 4.8 – 10.2 × 6.7, 1 female, 9.3 × 6.1 (USNM 154931), coral heads, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945.

Solomon Islands: 2 males, 12.6 × 8.3 – 13.7 × 8.8, 1 ovigerous female, 12.9 × 8.3 (USNM 154926), Solomon Islands, coll. United States Navy. — 1 female, 18.1 × 11.4 (USNM 41258), Solomon Islands, coll. Sealark Expedition, Sealark R/V, 1905. — 2 males, 18.9 × 11.9 – 20.1 × 12.8 (UF 3323), Stn. ZZZ-087901, 3–5 m, among rocks, Near Nusatupe Island, Ghizo Island, Solomon Islands, coll. H. Conley, 25 February 2002. — 1 female, 13.7 × 8.7 (UF 3345), Stn. ZZZ-087896, 3–6 m, under coral, Near Toa Maru or/and on East side of Nusatupe Island, Solomon Islands, coll. H. Conley, 23 February 2002. — 1 female, 17.3 × 10.9 (UF 3201), Stn. ZZZ-087845, 3–5 m, among rocks, Ghizo, near Nusatupe Island, Solomon Islands, coll. H. Conley, 25 February 2002.

Marshall Islands: 1 female, 15.1 × 9.7 (USNM 154925), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 male, 18.8 × 12.0 (USNM 154924), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 male, 11.7 × 7.8 (USNM 266946), ocean side, Japtan Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. J. Garth, 14 July 1957.

Samoan Islands: 1 male, 19.9 × 12.2 (UF 3231*), Stn. VB-034a, 0–1 m, under rubble, reef flat, Tutuila Island, Samoa Islands, American Samoa, coll. V. Bonito, 22 October 2002. — (?)1 male, 22.1 × 13.9 (USNM 23141*), Samoan Islands, South Pacific Ocean, coll. C. Eliot. — (?)1 male, 23.8 × 14.3, 1 female, 17.9 × 11.4 (USNM 154905), coral reef, Apia, Upolu Island, Western Samoa, South Pacific Ocean, coll. United States Fish Commission, July 1902.

Hawaiian Islands: 1 female, 13.7 × 8.8 (UF 12141), Stn. FFS-0087, 23.8732° -166.2348°, 4 m, under rocks, reef crest, French Frigate Shoals, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 16 October 2006. — 1 male, 6.0 × 3.8 (UF 12009*), Stn. FFS-OAHU-RUBEX, Oahu, Oahu Island, Hawaiian Islands, USA, coll., October 2006. — 2 females, 7.8 × 5.4 – 11.1 × 7.5 (UF 12336*), Stn. FFS-0091, 23.8733° -166.2347°, 15 m, back reef, French Frigate Shoals, French Frigate Shoals, Hawaiian Islands, USA, coll. R. Brainard & B. Zgliczynski, 16 October 2006. — (?) 1 female, 16.6 × 11.0 (ZRC 2000.0436), Kewalo, on sea wall, surf zone, Ala Moana area, Waikiki, Oahu, Hawaii, coll. P. Ng & S. Tan, 22 January 2000. — (?) 1 male, 13.5 × 8.9, 1 female, 10.3 × 7.2, 1 ovigerous female, 13.9 × 9.2 (USNM 154914), Waikiki Marine Lab, Oahu Island, Hawaii, United States, coll. G. Mansfield, 12 February 1942. — (?) 1 male, 13.6 × 9.1 (USNM 154909), 5 miles SW of Kapoho, Hawaii Island, Hawaii, United States, coll. O. Degener, 25 September 1929. — (?) 1 male, 15.4 × 10.2, 1 female, 16.0 × 10.4 (USNM 154910), Milolii Island, Hawaii Island, Hawaii, United States, coll. Pohina, January 1930. — (?) 1 male, 14.0 × 8.9, 3 females, 6.2 × 4.3 – 9.3 × 6.3, 1 ovigerous female, 15.8 × 10.4 (USNM 154912), reef, Mokuleia, Oahu Island, Hawaii, United States, coll. O. Degener, 1938. — (?) 1 male, 16.5 × 10.8 (USNM 25350), reef in front of Honolulu, Oahu Island, Honolulu, Hawaii, United States, coll. United States Fish Expedition, 16 August 1901. — (?) 1 ovigerous female, 14.4 × 9.3 (USNM 68938), Hawaii, United States, coll. United States Fish Commission, Albatross R/V.

Marquesas Islands: 1 female, 25.7 × 15.8 (USNM 114938), Stn. NH-X, 2–5 m, Centroid 8 50 S 140 02 W, Anaho Bay, Nuku Hiva Island, Marquesas

Islands, French Polynesia, coll. National Geographic Marquesas Islands Expedition, 19 September 1967.

Society Islands: 1 male, 10.8 × 7.1 (UF 15586*), Stn. MIB_037, -17.49631° -149.75295°, 0 m, within reef matrix, exposed reef crest, Temae reef flat, Moorea Island, Society Islands, French Polynesia, coll. A. Anker *et al.*, 15 October 2008. — 1 male, 6.4 × 4.3 (UF 15629*), Stn. MIB_041, -17.48037° -149.85286°, 10–12 m, under rocks, outer reef slope, rubble bed, mid N coast, off W of Sheraton Hotel, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al.*, 16 October 2008. — 1 male, 5.5 × 3.6 (UF 9808*), Stn. GP-Loc-871, -17.4964° -149.7528°, 0–0.5 m, within coralline reef framework, reef crest of narrow oceanic reef flat, Narrow Reef Flat Around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. G. Paulay, 29 June 2006. — 1 female, 5.7 × 3.8 (UF 15628), Stn. MIB_041, -17.48037° -149.85286°, 10–12 m, under rocks, outer reef slope, rubble bed, mid N coast, off W of Sheraton Hotel, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al.*, 16 October 2008. — (?) 3 females, 7.9 × 5.0 – 16.6 × 10.2 (USNM 154920), lagoon side of reef, W of Motu Tapu, Bora Bora, Society Islands, coll. Bredin Pacific Expedition, 25 April 1957. — (?) 1 female, 19.5 × 12.0 (USNM 154922), reef opposite Point Teanatira, Nuarei Bay, Moorea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 12 May 1957. — (?) 1 female, 9.8 × 6.4 (USNM 154919), reef NW of Motu Uta Island, Papeete Harbor, Tahiti, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 20 April 1957. — (?) 1 female, 13.6 × 8.9 (USNM 154921), coral, SW of Vaiorea Island, Bourayne Bay, Huahine, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 1 May 1957.

Diagnosis. Carapace (Pl. 19B) transversely hexagonal, ca. 1.5–1.6 times broad as long (ca. 1.7 in large specimens); dorsal surface convex, appearing smooth without magnification, granulate; medial regions defined by shallow or deep furrow; lateral regions defined by deep, sometimes punctate furrows,; 2M, 3M entire. Front (Pl. 19C) broad; submedian lobes convex, joining mesially to form shallow, V-shaped notch, separated from small lateral lobes by concavity. Anterolateral margin with 4 teeth excluding outer supraorbital tooth; tooth 1 low, obtuse, rounded; tooth 2 large, obtuse; tooth 3 large, rounded or spine tipped; tooth 4 spine tipped, anteriorly directed. Anterolateral angle of basal antennal segment not entering orbital hiatus, flagellum free to enter orbit. Pterygostomial region minutely granulate, without setae. Chelipeds (Pl. 19E, F) subequal, long, external surfaces smooth, spinose or with large protuberances; immovable finger with black pigment extending 1/2 length of lower margin; dactylus long. Ambulatory legs (Pl. 19A) moderately long, stout, setose; extensor surface covered with plumose and simple setae, lined with sharp, arched spines; tip of dactylus with single terminal, pigmented spine and two small, downward-pointing, subdistal spines. Male thoracic sternum (Pl. 19D) minutely granulate, without setae. Male abdomen (Pl. 19D) long, narrow; somite 6 longer than broad; telson longer than broad. G1 (Pl. 40D) moderately stout, laterally compressed; with ca. 14 long, simple distal setae, few short spines; apex spatulate, longitudinally hollowed.

Remarks. *Cyclodius nitidus* has one junior synonym: *Cyc. sculptus*. Gordon (1934: 39) stated that *Cyc. sculptus* was likely a junior synonym of *Cyc. nitidus* and discussed several characters that she regarded as intraspecific variation—e.g., tubercles on the external surface of the chelae, lobulation and width of the carapace, convexity of the front, and spination of the G1 (Pls 19A–C, E, F, 40D, 22A–C, E, F, 41C). Subsequently, Forest & Guinot (1961: 115) determined that these features amounted to intraspecific variation, and formally synonymized the two species after examining A. Milne

Edward's (1873) type series as well as *Cyc. nitidus* and *Cyc. sculptus* specimens from Hawaii to Madagascar. They also designated a lectotype from the Seychelles.

Cyclodius nitidus differs from other *Cyclodius* species in having a relatively wide carapace with smooth, deeply defined regions, densely setose ambulatory legs, and distinct G1 morphology (Pls 19A, B, 40D).

Distribution*.* Based on COXI sequence data, *Cyc. nitidus* is recorded from Western Australia, Indonesia, the Philippines, Japan, the Great Barrier Reef, and the Samoan Islands (Pl. 53B).

Cyclodius obscurus (Hombron & Jacquinot, 1846)

Pls (20, 41A)

Chlorodius obscurus Hombron & Jacquinot 1846: 26: pl. 3, fig. 4 [Samoa]. — ?DANA 1852b: 207 [Fiji Is.; Tahiti, Society Islands; Upolu, Samoa; Balabac Passage north of Borneo]; 1855, pl. 11, fig. 10 [Atlas].

Phymodius obscurus A. Milne-Edwards 1873: 220 [New Caledonia]. — Richters 1880: 148 [Iles Fouquets]. — De Man 1880: 174 [Djeddah, Saudi Arabia]. — ?Rathbun 1906: 858 [Hawaiian Is.]. — ?Edmondson 1946: 296 [Hawaiian Is.]; 1962: 278, fig. 20 d [Hawaiian Is.]. — Holthuis 1953: 24 [Onotoa, Gilbert Islands].

Cyclodius obscurus ?Felder & Thoma 2010: 136 [Hawaii]. — Davie 2002: 521 [List]. — Ng *et al*. 2008: 197 [List].

Chlorodius monticulosus Dana 1852a: 79 [Review]; 1852b: 206 [Fiji; Tahiti; Upolu, Samoa; Balabac Strait, Philippines]; 1855: pl. 11, fig. 9a–f [Atlas]. — Stimpson 1858: 34 (31) [Ryukyu Is and Bonin I., Japan; Tahiti]; 1907:

50 [Bonin Is, Ryukyu Is, Japan; Tahiti]. — Muller 1887: 474 [Trincomali, Sri Lanka].

Phymodius monticulosus Henderson 1893: 363 [Toothukudi, India]. — Alcock 1898: 163 [Nicobar Islands]. — Nobili 1905c: 490 [Key]; 1906c: 264 [Red Sea]. — Lenz 1910: 550 [Prunes Seamount(?) and Europa Island, Madagascar]. — Klunzinger 1913: 226 (130) [Red Sea]. — Bouvier 1915: 276 (99) [Mauritius]. — ?Balss 1924a: 10 [Sharm el-Sheikh]. — Gravely 1927: 145, pl. 21, fig. 23 [Key]. — Gordon 1934: 34, fig. 17 a-a', 18 a, 19 a [Port Loyd, Bonin Is.; Fakarava I.; Tuamotus; Butaritari I.; Tongatabu; Honolulu(?) and Coconut I.(?), Hawaii; Northwest I., Australia; Upolu, Samoan Is.; Zamboanga, Philippines; Aden, Yemen; Madagascar; Abrolhos, Australia; Masfield I.(?)]. — Barnard 1947: 364 [List]; 1950: 217, fig. 40 A-H [Delagoa Bay, South Africa]. — Tweedie 1950b: 122 [Cocos (Keeling) Islands]. — Guinot 1958a: 93 [Mayotte]; 1967c: 267 [List]. — Forest & Guinot 1961: 106, pl. 10, fig. 1-6 [Tahiti]. — Michel 1964: 28 [Mauritius]. — Derijard 1966: 168, fig. 9-11 [Europa]. — Sankarankutty 1966a: 351 [Pulli I., India]; 1966b: 50 [Mauritius; Maldives]. — Serène 1968: 81 [List]; 1984: 250–251, fig. 156, 157, XXXV A [Tamatave and Tulear, Madagascar; Ile Europa; Mombasa Kenya]. — Takeda & Nunomura 1976: 73 [Itot Maitre, Ile des Pins, Poum, and Ilot Mouac (in the vicinity of Pins), New Caledonia]. — Takeda & Miyake 1976: 110 [Ogasawara Is., Japan]. — Serène *et al.* 1976: 18 [Ambon, Indonesia]. — Chen & Lan 1978: 273, pl. 6, fig. 21 [Xisha Islands]. — Thomassin 1978: annexe 3, 64 [Tulear, Madagascar]. — Garth & Kim 1983: 686 [Marongas I., Philippines; Tikola Peninsula., Indonesia]. — Dai *et al*. 1986: 312, pl. 44(6), fig. 167A(3) [Review]. — Titgen 1987: 108 [O'ahu]. — Dai & Yang 1991: 335, pl. 44(6), fig. 167A(3) [Review]. — ?Coles *et al.* 2002a: 271, 334 [Oahu, Hawaii]. — Coles *et al*. 2002b: 140 [List].

Chlorodius dehanni Heller 1865: 19 (part) [Tahiti].

Cyclodius (*Cyclodius*) *ornatus* Dana, 1852a: 80 [Sulu, Philippines]; 1852b: 223 [Sulu Sea, Balabac Strait, Philippines]; 1855: pl. 12, fig. 11a–g [Atlas].

Chlorodopsis (Cyclodius) ornatus Alcock 1898: 171 [Andaman Islands, India]. — ?Borradaile 1900: 588 [Funafuti, Rotuma]; 1902: 262 [Male, Goifurfehundu, and South Mahlos, Lakshadweep]. — Balss 1834b: (part) 515 [Tamatave, Diego, and Tulear, Madagascar; Reunion Island; Mahe, Seychelles].

Cyclodius ornatus Nobili 1906c: 271 [Djibouti]; 1907: 397 [Fakahina, Marutea Sud, Tuamotu Archipelago]. — Rathbun 1907: 51, pl. 5, fig. 5, pl. 7, fig. 8 [Fakarava I.; Papeete; Butaritari I.]. — Klunzinger 1913 [Review]. — ?Edmondson 1925: 48. — Holthuis 1953: 18 [Onotoa, Gilbert Islands; Likiep Atoll, Marshall Islands].

Phymodius perlatus Nobili 1905c: 487, pl. 12, fig. 3 [New Guinea]. — Serène 1968: 81 [List].

Phymodius ungulatus, Laurie 1915: 450 [Sudan, Red Sea]. — (?)Balss 1924a: 10 [Tor, Senafir, Abu Somer?, Koseir, Berenice, Jambo?, Haleib?, Djeddah, Lidth?, Sarso I., Massaua, Cameran?, Djebel Zukur, Dahab, Habban, Ravaya?, Mersa Scheikh?]. — Sankarankutty 1962: 136, fig. 34-35 [Car Nicobar and South Andaman, India]. [not *Phymodius ungulatus* (H. Milne Edwards, 1834)]

Material examined. *Tanzania:* 1 male, 18.6 × 13.3, 1 female, 19.2 × 13.9 (USNM 81387), Zanzibar, Tanzania, coll. E. Ropes. — 2 males, 19.9 × 14.2 – 26.8 × 19.2, 1 female, 23.9 × 16.7 (USNM 1188418), Zanzibar, Tanzania, coll. E. Ropes.

Djibouti: 1 male, 15.1 × 11.0 (UF 32747), Stn. DJRS-001, 11.6012° 43.15895°, 0–2 m, fringing sand flat w/ some scuzzy seagrass, Djibouti city, in front of Sheraton Hotel, Djibouti, coll. G. Paulay, 26 September 2012.

Reunion: 1 male, 19.7 × 14.1 (UF 12568*), Stn. SWIO-FM31, -21.0941° 55.2347°, 0–2 m, La Saline, Planch'Alizé, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 23 July 2007.

Cocos (Keeling) Island: 8 males, 15.3 × 11.4 – 30.7 × 21.3, 1 ovigerous female, 16.4 × 12.2 (ZRC 1965.11.11.1–9), Cocos-Keeling Islands, coll. 1941.

Indonesia: 1 male, 13.1 × 10.1 (ZRC 2013.1681), BALI-0103, Bali, Indonesia. — 1 male, 16.1 × 11.9 (ZRC 2013.1682), BALI-0010, Bali, Indonesia.

Australia: 1 female, 13.6 × 9.9, (ZRC 2013.1684), NING 0123, Ningaloo Reef, Western Australia, Australia, 2010. — 3 males, 17.0 × 12.5 – 23.3 × 16.5, 1 female, 19.9 × 14.1, 1 ovigerous female, 21.4 × 15.3 (USNM 96938), near Cairns, Green Island, Great Barrier Reef, Queensland, Australia, coll. J. Howard, 1953. — 1 male, 27.6 × 19.6 (USNM 96937), coral reef flat, Heron Island, Capricorn Group, Great Barrier Reef, coll. J. Howard, 1953. — 3 males, 10.9 × 8.3 – 25.1 × 17.6, 2 females, 14.4 × 10.8 – 20.4 × 14.4 (USNM 64638), coral reef flat, Northwest Island, Capricorn Group, Great Barrier Reef, Queensland, Australia, coll. December 1925. — 1 female, 17.5 × 12.72 (UF 25408*), AUST-5776, HI09-071, 1–4 m, -23.4444° 151.9504°, Heron Lagoon, Heron Island, coll. R. Lasley & F. Michonneau. — 1 male, 9.7 × 7.3 (UF 25771*), AUST-6321, HI09-105, 1–2 m, -23.4617° 151.8868°, Heron Island, coll. R. Lasley, 25 November 2009. — 1 female, 7.8 × 6.0 (UF 22101*), AUST-3629, NIN09-St-53, 5–10 m, -22.493° 113.7258°, in rock, lagoon, Windabandy Point, Ningaloo Reef, Western Australia, Australia, coll. R. Lasley, CReefs Expedition, May 2009. — 1 male, 34.0 × 23.5, 1 female, 30.4 × 20.7 (USNM 96936), on coral reef flat, Hayman Island, Cumberland Islands, Great Barrier Reef, Queensland, Australia, coll. J. Howard, 1953. — 1 juvenile (UF 24955), Stn. HI09-020, -23.44491667° 151.9337667, 3–3 m, Heron Island, Shark Bay, Queensland, Australia, coll. K. Schnabel, *et al*., 14 November 2009. — 1 female, 20.6 × 14.8 (UF 24972*), Stn. HI09-025, -23.26011667 151.91691667, 3–6 m, in rubble, shallow patch reefs, Heron Island, Broomfield Reef, Queensland, Australia, coll. S. McKeon & F. Michonneau, 15 November 2009. — 1 female, 10.3 × 7.6 (UF 25602*), Stn. HI09-080, -23.44478333° 151.9504333°, 4 m, sand, Heron Island, Heron Lagoon, Queensland, Australia, coll. 22 November 2009. — 1 female, 11.0 × 8.1 (UF 25781*), Stn. HI09-131, -23° 152°, Heron Island, Queensland, Australia, coll. November 2009. — 1 female, 24.3 × 16.6 (UF 25782*), Stn. HI09-105, -23.46171667° 151.8868333°, 1–2 m, Heron Island, Queensland, Australia, coll. R. Lasley, 25 November 2009. — 1 juvenile (UF 27921), Stn. NR10-043, -22.67039° 113.64955°, 2–3 m, in rubble, Ningaloo Reef, right off Ningaloo station, Western Australia, Australia, coll. A. Anker, 23 May 2010.

Philippines: 1 male, 22.40 × 15.60, 1 female (ZRC 2013.0738), Stn M34, 0–1 m, 9°43.8’N 123°52.7’E, nipa palms and sandbar; salinity 10%, Abatan River, Bohol Island, Philippines, coll. Panglao Expedition, 25 June 2004. — 1 female, 21.4 × 15.4 (ZRC 2013.1679), R66, Panglao Philippines, 2004. — 1 female, 15.1 × 11.1 (ZRC 2013.1680), B34, Panglao, Philippines, 2004. — 3 males, 18.1 × 13.5 – 19.9 × 14.6 (USNM 154891), shore, Morongas Island, Sulu Archipelago, Sulu, Philippines, coll. Albatross R/V, 10 February 1908. — 1 ovigerous female, 11.5 × 8.3 (USNM 1181372), 14 03 45 N 120 16 30 E, W of Fortune Island, Luzon Island, Cavite, Philippines, China Sea, coll. United States Fish Commission, Philippines Expedition, Albatross R/V, 15 January 1908.

Japan: 1 male, 23.3 × 17.0 (USNM 13903), Port Lloyd, Bonin Islands, Japan. — 1 male, 23.4 × 16.5 (USNM 13904), Port Lloyd, Bonin Islands, Japan. — 1 male, 18.1 × 13.0 (UF 26990*), Stn. GUOK10-St-071, 26.21218° 127.664291°, 1–8 m, silty harbor, river mouth, wharfs, Okinawa, Naha Harbor, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 16 July 2010. — 19.3 × 13.7 (UF 26936*), Stn. GUOK10-St-068, 24.373801° 123.75053°, 0–4 m, mostly under dead *Acropora* tables, sheltered, shallow bay with *Acropora* reef patches, Iriomote, Midara Beach, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 11 July 2010.

Caroline Islands: 1 male, 12.2 × 9.2, 1 ovigerous female, 16.2 × 11.6 (USNM 33294), 5 19 N 162 59 E, Kusaie, Kosrae Island, Caroline Islands, Micronesia, coll. Albatross R/V, 8 February 1900. — 1 male, 17.7 × 12.8 (USNM 1184692), 1 m, at causeway, off S end of seawall, Malakal, Palau, coll. R. Kropp, 20 July 1984. — 1 male, 20.3 × 14.6 (USNM 154892), 7 02 51 N 134 17 42 E, boat channel E of Peleliu Island, Palau, coll. F. Bayer, 24 July 1955. — 1 male, 13.6 × 10.1 (USNM 106543), lagoon reef, Hare Island, Kapingamarangi Atoll, Pohnpei Islands, Caroline Islands, Micronesia, coll. C. Hand, Fifth Pacific Atoll Survey, 20 July 1954. — 1 male, 21.4 × 15.7 (UF 3897*), Stn. BPAL-090, 7.3135° 134.4875°, 0–3 m, under rocks and exposed, Hidden Cove Along N Shore of Ulebeschel Island, Iwayama Bay System: "bay of The Dragon Palace", Palau, coll. G. Paulay, 5 March 2003. — 1 male, 16.0 × 12.2 (UF 5874), Stn. JAS-PON-082, 6.99° 158.23°, 0–1 m, under rock, channel and seagrass/coral flat on reef side, Lenger Island, Next to Japanese Dock at Clam Hatchery, Pohnpei Island, Caroline Islands, Federated States of Micronesia, coll. J. Starmer, 14 March 2003.

Solomon Islands: 5 males, 16.2 × 12.2 – 23.2 × 16.9 (USNM 1181280), NE of Malaita Island, Sikiana Island, Solomon Islands, coll. Templeton Crocker Expedition, 12 May 1933. — 1 ovigerous female, 11.1 ×

8.1 (UF 29676*), Stn. ZZZ-087896, 3–6 m, under coral, Near Toa Maru or/and on East side of Nusatupe Island, Solomon Islands, coll. H. Conley, 23 February 2002.

New Caledonia: 1 male, 12.0 × 9.1 (UF 3439), BNEC-001, 0.5–5 m, sand, fringing reef, Baie de Citron, Noumea, New Caledonia, coll. G. Paulay, 1 January 1999. — 1 male, 19.8 × 14.3 (UF 17995*), Stn. NC09-St-6, -22.313203° 166.457452°, 0–1 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 10 March 2009.

Vanuatu: 1 male, 13.3 × 10.0, 1 female, 13.5 × 10.3 (ZRC 2013.1683), Stn. ZB36, Vanuatu, coll. Santo 2006.

Marshall Islands: 1 female, 11.1 × 8.4 (USNM 93971), inner edge of reef, between Nado Island and Likiep Island, Likiep Atoll, Ratak Chain, Marshall Islands, coll. F. MacNeil, December 1951. — 2 males, 10.7 × 7.8 – 11.0 × 8.6 (USNM 266944), Enewetak Atoll, Ralik Chain, Marshall Islands, coll. A. Banner, 23 February 1957. — 1 male, 22.5 × 16.5 (UF 2182*), Stn. BMAJ-007, lagoon slope, in front of Outrigger Hotel, Majuro Atoll, Marshall Islands, Republic of the Marshall Islands, coll. G. Paulay, 9 November 1997.

Kiribati: 1 male, 25.3 × 17.9, 2 females, 12.0 × 8.9 – 14.9 × 10.7 (USNM 33403), Tari Island, coll. Albatross R/V, 6 January 1900. — 6 males, 11.4 × 8.5 – 19.2 × 13.6, 4 females, 13.7 × 10.3 – 17.2 × 12.4 (USNM 91641), inner lagoon, Fanning Island, Line Islands, Kiribati, coll. F. Baker & C. Baker, 16 December 1913. — 1 female, 12.4 × 9.3 (USNM 93974), 1 52 S, 175 34 E, S end of northern main island, Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 8 August 1951. — 1 male, 15.4 × 11.3, 1 female, 13.8 × 10.2 (USNM 94203), Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 9 August 1951.

Fiji: 1 male, 23.4 × 16.7 (USNM 91645), Nukulau Island, Fiji, coll. A. Herre, 15 March 1929.

Tonga: 1 male, 22.1 × 15.5 (USNM 1181266), Niuafou Island, Vava'u Group, Tonga, coll. H. Kellers, U.S. Navy Eclipse Expedition to Niuafou Tonga, 1 October 1930. — 1 male, 20.7 × 15.1 (USNM 33402), Tongatapu Island, Tongatapu Group, Tonga, coll. Albatross R/V, 30 November 1899.

Samoan Islands: 1 ovigerous female, 13.0 × 9.8 (USNM 134580), Pago Pago, Tutuila, American Samoa, coll. Samoan Investigations 1902, Albatross R/V, August 1902. — 2 males, 19.1 × 13.5 – 24.5 × 17.9 (USNM 91638), outer coral reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, 1 July 1902.

Japan: 1 male, 16.0 × 11.3 (ZRC 1992.4995), Bise Village, coral reef, Motobu-Cho, Okinawa, Japan, coll. P. Ng, April 1992.

Hawaii: 1 ovigerous female, 15.5 × 11.3 (ZRC 2000.0429), intertidal area, Maipalaoa Beach, near Maili Point, Maili Waianae coast, leeward side of Oahu, Hawaii, coll. P. Ng & S. Tan, 22 Jan 2000. — 1 male, 21.9 × 14.6 (USNM 64182), Coconut Island, Kaneohe Bay, Oahu, Hawaii, United States, coll. P. Gallsoff, July 1930. — 2 males, 21.9 × 15.2 – 23.6 × 16.3 (USNM 91639), Milolii, Hawaiian Island, Hawaii, United States, coll. Pohina, January 1930. — 1 male, 17.0 × 11.7 (USNM 29532), Hilo, Hawaii Island, Hawaii, United States, coll. Albatross R/V. — 1 male, 14.5 × 10.4, 1 female, 15.8 × 11.1 (USNM 99164), Waikiki Reef, Oahu Island, Hawaii, United States, coll. C. Cutress, 4 March 1950. — 1 male, 12.7 × 8.9, 1 ovigerous female, 17.5 × 12.2 (USNM 25353), reef in front of Honolulu, Oahu Island, Honolulu, Hawaii, United States, coll. United States Fish Commission, 16 August 1901 – 17 August 1901. — 2 males, 16.6 × 12.1 – 17.0 × 12.1 (USNM 29534), 21 05 00 N 157 01 40 W, S of Kaunakakai, Molokai Island, Hawaii, United States, coll. United States Fish Commission, Hawaiian Explorations, Albatross R/V, 2 April 1902. — 1 male, 24.0 × 16.4 (USNM 81416), Kaneohe Bay, Oahu Island, Hawaii, United States, coll. C. Edmondson, 1936. — 1 female, 9.9 × 7.1 (UF

23081*), Stn. Pittman-1091015.4, 1–3 m, harbor, breakwater near boat launching ramp, Kahului Harbor, Maui Island, Hawaiian Islands, USA, coll. C. Pittman, 15 October 2009. — 1 male, 28.9 × 19.9 (UF 8597*), Stn. BOAHU-21, 19.7325° -155.07139°, under rocks, silty reef flat, Kaneohe Bay, Coconut Island, NE Side, Oahu Island, Hawaiian Islands, USA, coll. G. Paulay, 17 August 2004. — 1 male, 25.7 × 17.1 (UF 8781*), Stn. GP-Loc-855, 21.43528333° -157.78878333°, 0–0.5 m, from *Porites compressa*, etc. crevices at night, seaward margin of reef flat, Kaneohe Bay, Coconut Island, Oahu Island, Hawaiian Islands, USA, coll. G. Paulay, 28 February 2006. — 3 males, 17.7 × 12.4 – 20.3 × 14.4, 1 female, 17.4 × 11.9, 1 ovigerous female, 15.6 × 11.1 (USNM 17308), Oahu Island, Hawaii, Centroid: 21 18 N 157 51 W, coll. Albatross.

Tuamotu Islands: 8 males, 5.8 × 4.5 – 28.4 × 19.6, 10 females, 8.1 × 6.0 – 19.9 × 14.3, 2 ovigerous females, 11.7 × 8.6 – 16.9 × 12.5 (USNM 33405), outer reef, Fakarava Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 12 October 1899. — 4 males, 14.7 × 10.8 – 18.4 × 13.2, 2 females, 10.2 × 7.7 – 10.9 × 8.2 (USNM 154893), shore, lagoon, Maiai Island, Tikehau Atoll, Tuamotu Archipelago, French Polynesia, coll. Bredin Pacific Expedition, 13 April 1957. — 1 female, 17.5 × 12.8 (UF 18537*), Bacchet-001, reef flat, Mekemo, Makemo Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, April 2009. — 1 female, 16.0 × 11.5 (UF 18536*), Stn. Bacchet-001, reef flat, Mekemo, Makemo Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, April 2009.

Society Islands: 1 male, 17.5 × 12.6, 1 female, 16.1 × 12.4 (USNM 81392), Society Islands, French Polynesia.

Diagnosis. Carapace (Pl. 20B) transversely hexagonal, ca. 1.4 times broad as long; dorsal surface convex, appearing smooth without magnification, minutely granulate; regions defined by broad depressions; 2M divided longitudinally; 3M tripartite, shallowly divided. Front (Pl. 20C) markedly broad; submedian lobes relatively straight or convex; joining medially to form V-shaped notch; lateral lobes relatively small. Anterolateral margin with 4 obtuse, lobular teeth excluding outer supraorbital tooth; tooth 1 smallest; teeth 2, 3 large; tooth 4 small. Anterolateral angle of basal antennal segment entering less than halfway into orbital hiatus, flagellum free to enter orbit. Pterygostomial region granulate with posterior plumose setae in large specimens. Chelipeds (Pl. 20E, F) unequal, stout, long, external surfaces appearing smooth to naked eye, granulate, or bearing granulate protuberances; immovable finger with black pigment extending 1/2 length of lower margin and distally unto external surface; dactylus convex, fingers gaping. Ambulatory legs (Pl. 20A) short, stout, with numerous plumose setae, pubescence; extensor surface lined with arched spines or granules; tip of dactylus generally trifid, pigmented spine usually greater than or equal to downward-pointing, subdistal spines. Male thoracic sternum (Pl. 20D) minutely granulate, with few or no setae, appearing smooth without magnification. Male abdomen (Pl. 20D) long, narrow; somite 6 longer than broad; telson longer than broad, lateral margins slightly concave. G1 (Pl. 41A) long, narrow; with several stout, proximally pointing subdistal setae, usually two long, narrow emergent setae; apex laterally flattened or curved, tip rounded.

Remarks. Forest & Guinot (1961: 106) gave extensive evidence for the synonymy of *Cyclodius ornatus* Dana, 1852 and *Chlorodius obscurus* Hombron & Jacquinot, 1846 with *Chlorodius monticulosus* Dana, 1852. There had been confusion over the dates of Hombron & Jacquinot's (1846) Atlas, which contains a plate with the holotype specimen of *Cyc. obscurus.* Subsequently, Clark & Crosnier (2000) showed that the date of Hombron & Jacquinot's work was 1846, giving priority to the name *Chlorodius obscurus*.

Forest & Guinot (1961) also sorted out misidentified specimens of *Cyc. obscurus* in literature and collections, many of which were identified as *Cyc. ungulatus*. These two species are similar in general habitus of the carapace, and had been synonymized by Rathbun (1907: 47) (Pls 20A, 23A). The regions of the carapace of both species have a smooth, bulging look and are separated by deep depressions. They also have similarly long chelipeds with gaping fingers. After examining a large selection of specimens, Gordon (1934) regarded *Cyc. obscurus* and *Cyc. ungulatus* as distinct species and extensively discussed their morphological differences, providing elucidative character tables for distinguishing between adult and juvenile, and male and female specimens. The two species have markedly different G1 morphologies (Pls 41A, D). Furthermore, the morphology of the front is different (Pls 20B, 23B). *Cyclodius obscurus* has lateral lobes of the front that are more projecting with a wider 2F (versus less projecting lateral lobes and narrower 2F in *Cyc. ungulatus*) (Gordon 1934: fig. 17). In addition, *Cyc. obscurus* has a proportionally narrower carapace with a more convex, shallowly areolated gastric region (versus broader with a flatter gastric region with deep areolae). See Gordon (1934) for more diagnostic features.

The name *Phymodius perlatus* Nobili, 1905 has not been used since the species' original description based on two specimens from New Guinea. Nobili (1905) provided a key to the species of the genus *Phymodius* (= *Cyclodius*) where he distinguished *Phymodius perlatus* based on the granulation and lack of setae of the ambulatory legs, granulation of the chelipeds, and denticulate anterolateral teeth of the carapace. With the exception of the ambulatory leg setae, Forest & Guinot (1961) discuss these features as variable in female, male, adult and juvenile specimens of *Phymodius monticulosus* (= *Cyc. obscurus*). Additionally, Nobili's (1905: pl. 12, fig. 3) figure of the holotype is indistinguishable from young and female specimens of *Cyc. obscurus* (e.g., UF 25408, UF 18537, UF 3439, etc.). The lack of setae on the ambulatory legs is the only distinguishing feature that is not commonly within the range of variation in *Cyc. obscurus*. However, many specimens have very few setae on their ambulatory legs, and it is not difficult to imagine finding one without setae due to variation or wear. Furthermore, Forest & Guinot's (1961: pl. 10, fig. 2) photograph of a juvenile *Cyc. obscurus* specimen does not appear to have setae on its ambulatory leg. Based on these observations, *Phymodius perlatus* is regarded as a junior synonym of *Cyc. obscurus.*

Distribution. *Cyclodius obscurus* has a widespread IWP distribution from the east coast of Africa and the Red Sea to Hawaii and French Polynesia (Pl. 49B).

Cyclodius paumotensis (Rathbun, 1907)

Pls (21, 41B, 49D)

Pilodius paumotensis Rathbun 1907: 52, pl. 8, fig. 2, 2a, 2b [Type locality = Makemo I., Tuamotu; also from Fakarava I.]; 1911: 227 [Salomon]. — Balss 1938a: 58 [Aranuka, Tamana and Apamama, Gilbert Islands]. — Holthuis 1953: 25 [Likiep Atoll, Marshall Islands]. — Guinot 1962b: 237, fig. 14a, b [Addu Atoll, Maldives]. — Serène 1968: 80 [List]; 1984: 241, figs 143d, 145, pl. 33d [Itampolo, Madagascar; Reunion Island]. — Takeda & Miyake 1968: 7, pl. 1, fig. F [Okinawa]. — Serène 1968: 80 [list]. — Peyrot-Clausade and Serène 1976: 1357, pl. 4D [Madagascar]. — Takeda & Miyake 1976: 110 [Ogasawara Is., Japan]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]; 1989: 113 [Tikehau, Tuamotu]. — Ribes 1978: 127 [Reunion I.]. — Clark & Galil 1993: 1143, figs 10A–G, 35B, 43A [Delagoa Bay, Mozambique; Reunion I.; Tuléar and Itampolo, Madagascar; Mauritius; Addu Atoll, Maldives; Coin, Chagos Archipelago; Guam; Likiep Atoll, Marshall Is; Tamana, Gilbert Is; Oahu, Hawaiian Is.; Marutea, Makemo, and Fakarava, Tuamotu Archipelago; Bora Bora; Eua I., Tonga].

Chlorodopsis granulatus, Nobili 1907: 46 [Marutea Sud, Tuamotu Islands]. (not *Pilodius granulatus* Stimpson, 1858)

Chlorodopsis oahuensis Edmondson 1962: 270 [Oahu, Hawaii].

Chlorodopsis pilumnoides, Barnard 1955: 3 (part). — Michel 1964: 24 [Mauritius]. — Guinot 1967: 268 (part) [List]. (not *Pilodius pilumnoides* White, 1848)

Material examined. *Mozambique:* 2 males, 10.5 × 6.6 – 11.1 × 7.2, 1 female, 11.2 × 7.2 (ZRC 1999.1211), Inhaca, Mozambique, coll. J. Paula, 16 April 1995. — 1 ovigerous female, 9.2 × 5.9 (ZRC 1999.1210), Inhaca, Mozambique, coll. J. Paula, 16 January 1994.

Solomon Islands: 1 female, 7.2 × 4.5 (USNM 41270), Solomon Islands, coll. Sealark Expedition, Sealark R/V, 1905.

Mariana Islands: 1 male, 6.3 × 4.1 (USNM 11881313), outer ridge, Ypan, Guam, coll. R. Kropp & J. Dominguez, 23 September 1984. — 1 male, 5.7 × 3.7, 1 female, 6.8 × 4.4 (USNM 1188361), S of cut, Guam, Pago Bay, coll. R. Kropp, 11 August 1984. — 1 male, 4.0 × 2.7, 1 female, 3.9 × 2.2, 1 ovigerous female, 5.4 × 3.6, 1 juvenile (USNM 1184934), 0–1 m, from reef margin to N of bay, Guam, Toguan Bay, coll. J. Dominguez, 14 February 1984. — 1 ovigerous female, 8.3 × 5.3 (USNM 1181383), in coral, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945.

Marshall Islands: 5 males, 4.0 × 2.7 – 5.4 × 3.5, 1 female, 4.2 × 2.8, 1 ovigerous female, 7.0 × 4.6 (USNM 93999), Nado Island, Likiep Atoll, Ralik Chain, Marshall Islands, coll. R. Macneil, 1951. — 1 female, 6.0 × 4.0 (USNM 1181393), Bikini Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. Ladd & Tracy, 3 May 1946.

Niue Island: 1 female, 9.5 × 6.3, 3 juveniles (UF 2276), BNIUE-362, 5–15 m, undersides of rocks and substrate surface, outer reef slope, S of Wharf, Alofi Wharf, Niue, coll. B. Holthuis & G. Paulay, 14 October 1991.

Hawaiian Islands: 1 female, 6.5 × 4.2 (USNM 102199), Kawela Bay, Oahu Island, Hawaii, United States, coll. C. Edmondson. — 3 females, 7.6 × 4.9 – 9.0 × 6.0, 2 ovigerous females, 6.5 × 4.2 – 7.9 × 5.3 (USNM 48952), low tide, reef, Pukoo, Molokai Island, Hawaii, United States. — 2 females, 6.6 × 4.5 – 8.8 × 5.6 (USNM 56026), Waikiki Reef, Oahu Island, Hawaii, United States, coll. C. Edmondson, 1921.

Kiribati: 1 female, 7.4 × 5.0 (USNM 1181385), Sta. 7, Washington Island, Line Islands, Kiribati.

Society Islands: 7 males, 3.9 × 2.6 – 6.7 × 4.5, 2 females, 5.5 × 3.7 – 8.5 × 5.5 (USNM 1181380), Nuarei Bay, Moorea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 11 May 1957. — 1 male, 7.8 × 5.2 (UF 15600*), BMOO_2781, MIB_037, 0 m, -17.4963° -149.753°, rubble cracking, exposed reef crest, Temae reef flat, Moorea, Society Islands, French Polynesia, coll. A. Anker *et al.*, 15 October 2008. — 1 male, 7.9 × 5.2 (UF 9791*), BMOO-610, GP, Loc-871, 0–0.5 m, -17.4964° -149.7528°, by hand, within coralline reef framework, reef crest of narrow oceanic reef flat, around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. G. Paulay, 29 June 2006. — 1 damaged female (UF 9763*), 0-0.5 m, BMOO-670, GP-Loc-871, -17.4964° -149.7528°, by hand, within coralline reef framework, reef crest of narrow oceanic reef flat around Pt. Faupo, Moorea

Island, Society Islands, French Polynesia, coll. G. Paulay, 29 June 2006. — 1 male, 8.4 × 5.7, 2 females, 3.6 × 2.0 – 6.3 × 4.1 (USNM 1181375), lagoon side of reef, W of Motu Tapu, Bora Bora, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 25 April 1957.

Tuamotu Islands: 1 male, 6.3 × 4.2, 1 ovigerous female, 6.6 × 4.3 (USNM 33323), outer reef, Fakarava Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 12 October 1899. — 1 male, 6.4 × 4.4, 2 ovigerous females, 5.8 × 3.8 – 5.7 × 3.9 (UF 1594), Stn. BRNG-032, -14.98333° -147.61667, nestled in crevices in reef rock, outer reef flat, and reef crest, Avatoru Motu, off Far W Hoa, Rangiroa Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 22 October 2001. — 1 holotype male, 7.9 × 5.2, 1 female, 6.6 × 4.5, (USNM 32852), Reef, Makemo, Paumotus, coll. 21 October 1899.

Diagnosis. Carapace (Pl. 21B) transversely hexagonal, ca. 1.5 times broad as long; dorsal surface granulate. Regions granulate, well defined by relatively shallow furrows, covered with long and short simple, light-colored setae; 2M, 3M entire. Front (Pl. 21C) markedly broad; submedian lobes joining medially to form U-shaped indention, relatively straight medially, convex laterally; lateral lobes small. Anterolateral margin with four anteriorly directed spinose teeth excluding outer supraorbital tooth, separated by concave gaps; tooth 1 smallest, usually with two emergent spines, near outer supraorbital tooth but separated by small spines; tooth 2 largest with two anterior spines, one or two posterior spines; tooth 3 subequal in size to tooth 2, with one to three spines; tooth 4 small with one emergent spine, sometimes small secondary spines. Posterior and posterolateral margins with transverse rows of granules. Anterolateral angle of basal antennal segment entering less than halfway into orbital hiatus. Pterygostomial region minutely granulate with plumose setae diagonally from posterior to lateral surface. Chelipeds (Pl.

21E, F) subequal, stout, external surfaces granulate, with long, simple setae, palm relatively short; merus not extending far beyond anterolateral margin when apposed to carapace; pigmentation restricted to fixed finger; dactylus proximally relatively straight, distally convex. Ambulatory legs (Pl. 21A) relatively short, stout, with numerous simple setae, especially on extensor surface; extensor margin lined with short spines; tip of dactylus with large distal spine, pigmented, small subdistal spines. Male thoracic sternum (Pl. 21D) smooth, few setae and granules on anterolateral margin of sternite 4. Male abdomen (Pl. 21D) short, smooth; somites 3–5 fused, sometimes with faint sutures indicated; somite 6 ca. broad as long; telson ca. broad as long, barely reaching imaginary line between posterior margin of first ambulatory leg sternal condyles. G1 (Pl. 41B) stout; with ca. 5 long, simple, subdistal setae, numerous short spines; distal lobe ovate, tip pointed.

Remarks. *Cyclodius paumotensis* is easily distinguished from other *Cyclodius* specimens by its setose carapace and distinct G1 morphology (Pls 21B, 41B).

Distribution. *Cyclodius paumotensis* has a widespread IWP distribution from the east coast of Africa to Hawaii and French Polynesia. It has not been recorded from the Red Sea, Gulf of Aden, Persian Gulf, or Arabian Sea (Pl. 49D).

Cyclodius ungulatus (H. Milne Edwards, 1834)

Pls (23, 41D, 49C)

Chlorodius ungulatus H. Milne Edwards 1834: 400, pl. 16, fig. 6-8 [Australasia]. — Dana 1852b: 205 [Navigator Islands; Tahiti; Mangsi

Islands, Balabac Passage]; 1855: pl. 11, fig. 8 a, b [Atlas]. — Hess 1865: 135 [Australia].

Chlorodius gracilis Dana 1852. — Simpson 1907: 56 [coast of China, near Hong Kong].

Phymodius ungulatus A. Milne-Edwards 1873: 218 [New Caledonia]. — ?Kossmann 1877: 34 [Red Sea]. — Hilgendorf 1879: 790 [Ibo, Mozambique]. — Haswell 1882: 59 [Port Denison, Australia]. — Henderson 1893: 362 [Sri Lanka]. — Ortmann 1893: 464 [Upolu, Samoan Islands; Mauritius]; 1894b: 51 [Ambon I., Indonesia; Dar es Salaam, Tanzania]. — Alcock & Anderson 1894: 200 [off Tamil Nadu]. — Alcock 1898: 162 [Andaman Islands, India; Sri Lanka]. — Borradaile 1900: 587 [Rotuma]; ?1902 [Maldives and Laccadives]. — Calman 1900: 11 [Torres Strait]. — Nobili 1901b: 14; 1905c: 490 [Key]; 1907: 393 [Mangareva I., Gambier Islands]. — De Man 1902: 618 [Ternate, Indonesia]. — Rathbun 1906: 857 [Honolulu, Hawaii]; 1907: 46, pl. 3, 4 (part) [Makemo I.; Fakarava I.; Rangiroa I.; Tahiti; Bora Bora; Butaritari]; 1911: 225 [Salomon, Egmont Reef, Diego Garcia]. — Grant & McCulloch 1906: 13 [Mast Head I., Australia]. — Lenz 1905: 354 [Zanzibar, Tanzania; Bawi(?)]; 1910: 550 [St. Mary and Antongil Bay, Madagascar]. — Stebbing 1910: 299 [List]. — Klunzinger 1913: 225 (129), pl. 1, fig. 8 [Red Sea]. — Bouvier 1915: 275 (98) [Mauritius]. — Edmondson 1923a: 17 [Palymyra I.; Fanning I.]; 1925: 44 [Wake I., Pearl and Hermes Reef, Lisianski I., and Laysan I., Hawaiian Is.]; 1933: 250, fig. 152 d [Review]; 1962 278, fig. 23a [Hawaiian Is.]. — Balss 1938a: 55 [Aranuka, Tapitoea and Taritari, Gilbert Islands; Likieb and Jaliut, Marshall Islands; Viti Levu, Bau, Namuka, Fiji Island]. — Montgomery 1931: 442 [Long I., Abrolhos Is.]. — Ward 1932: 250 [Heron Island, Hoskyn Island, One Tree Island, Lady Musgrave Island and North West Island, Australia]; 1933a: 250;

1939: 10 [Savaii Island, Samoa]. — Boone 1934 (part): 140, pl. 76. — Gordon 1934: 36, fig. 17 b, pl., 18 b, 19 c [Bora Bora; Basilian Strait, Zamboanga, Little Santa Cruz I., Philippines; Seychelles; Apia, Samoan Is.; Madagascar; Sri Lanka; Banda Neira, Indonesia]. — Miyake 1936: 508 [Yaeyama, Japan]. — Sakai 1939: 509, pl. 97, fig. 4 [Loo Choo, Japan]; 1976, p. 463, pl. 165, fig. 1 [Yoron I., Ishigaki I., Taketomi I., Japan]. — Vatova 1943: 20 [Somalia]. — Stephensen 1946: 157 [List]. — Barnard 1950: 216, fig. 40 i, j [Natal Point, South Africa]. — Tweedie 1950a: 92 [Aur I., Malaysia]; 1950b: 122 [Cocos (Keeling) Islands]. — Holthuis 1953: 25 [Saipan, Mariana Islands; Onotoa and Bikati, Gilbert Islands; Otikaheru Island, Tuamotu Islands]. — Forest & Guinot 1961: 110, fig. 86 a, b; pl. 11, fig. 1-4: pl. 12, fig. 1-4; pl. 13, fig. 1-3; pl. 14, fig. 1-3 [Hikueru, Tuamotus Islands; Tahiti; Mangareva, Gambier Archipelago]. — Michel 1964: 29 [Mauritius]. — Derijard 1966: 168, fig. 12-14 [Europa]. — Sankarankutty 1966b: 50 [Mauritius]. — Guinot 1967c: 267 [List]. — McNeill 1968: 61 [Great Barrier Reef, Australia]. — Serène 1968: 81 [List]; 1977a: 51 [Seychelles]; 1984: 251–252 [Nosy Be, north west coast, Nosy Iranja, Fort-Dauphin, Madagascar; Iles Glorieuses, Ile Europa; Mayotte, Iles Comoros; Aldabra, Iles Seychelles]. — Takeda & Nunomura 1976: 74 [Kokopo (near Rabaul), New Britain; Guadalcanal (Honiali), Solomons; North Island and Saddle Island, Australia; Itol Mouac (in the vicinity of Poum), New Caledonia]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]; 1977b: 213 [Moorea]; 1989: 113 [Tikehau, Tuamotu]. — Chen & Lan 1978: 273, pl. 6, fig. 22 [Xisha Islands]. — Ribes 1978: 127 [Reunion I.]. — Kensley 1981: 45 [List]. — Garth & Kim 1983: 686 [Balayan Bay, Philippines]. — Dai *et al*. 1986: 312, pl. 45(1), fig. 167A(4) [Review]. — Dai & Yang 1991: 336, pl. 45(1), fig. 167A(4) [Review]. —

Coles *et al*. 2001: 54 [List]. — Coles *et al*. 2002a: 271, 334; 2002b: 140, 194 [Oahu, Hawaii].

Cyclodius ungulatus Davie 2002: 522 [List]. — Ng *et al.* 2008:197 [List].

Chlorodius (Cyclodius) gracilis Dana 1852a: 80.

Cyclodius gracilis Dana 1852b: 224 [Tutuila Island, Samoa]; 1855: pl. 12, fig. 12a–b. — Nobili 1907: 397 [Fakahina, Tuamotu Archipelago; Mangareva I., Gambier Is.]. — Rathbun 1907: 51, pl. 1, fig. 10, pl. 7, fig. 7 [Funafuti]. — Calman 1909: 705 [Christmas Island].

Chlorodius dehaani, Heller 1865: 19 (part). (not *Xantho dehaani* Krauss, 1843)

(?) *Phymodius granulatus,* Balss 1934b: 516 [Tulear, Madagascar; Mahe, Seychelles]; 1938a: 55 [Apamama, Aranuka, Tapitoea, Gilbert Islands; Jaluit, Likieb, and Ebon, Marshall Islands; Viti Levu and Namuka, Fiji Island]. — Ward 1942b: 98 [Chagos Archipelago, Salomon]. [not *Cyclodius granulatus* (Targioni-Tozzetti, 1877)]

Material examined. *Madagascar:* 1 male, 20.0 × 13.7 (UF 14607*), NBE-2086, MGNW-38, 1–6 m, -13.4292° 48.364°, N end of islet lagoonal fringing reef slope with sand and rubble, near Nosy Be, Trois Freres Islet, Madagascar, coll. A. Anker *et al.*, 20 May 2008. — 1 male, 15.4 × 10.9 (UF 14325*), Stn. MGNW-23, -13.4139° 48.3056°, 1–3 m, seagrass flat and adjacent sand/reef slope, Nosy Be, across bay from CNRO complex, off Lokobe Reserve, Madagascar, coll. A. Anker *et al.*, 16 May 2008. — 1 female, 11.9 × 8.5 (UF 14360*), Stn. MGNW-23, -13.4139° 48.3056°, 1–6 m, rubble, seagrass flat and adjacent sand/reef slope, Nosy Be, across bay from CNRO complex, off Lokobe Reserve, Madagascar, coll. G. Bakary *et al.*, 16 May 2008.

Seychelles: 2 males, 17.6 × 12.2 – 19.1 × 13.4, 2 females, 14.5 × 10.0 – 18.2 × 12.3 (USNM 41256),Coetivy Island, Seychelles, coll. Sealark Expedition, Sealark R/V, 1905.

Mascarene Islands: 1 male, 9.2 × 6.5 (UF 12586*), BREU-FM-0228-1, SWIO, 0–2 m, -21.1008° 55.2437°, Trou d'eau, La Saline, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 27 July 2007. — 1 ovigerous female, 11.2 × 8.0 (UF 12559*). — 1 ovigerous female, 12.5 × 8.7 (UF 12560*), Stn. SWIO-FM29, -21.0941° 55.2347°, 0–2 m, La Saline, Planch'Alizé, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 20 July 2007.

Cocos (Keeling) Island: 1 female, 24.8 × 16.2 (ZRC 2013.1672), Stn. CK2-21, Cocos (Keeling) Island.

Christmas Island: 1 male, 25.2 × 17.0 (ZRC 2013.1673), Stn. CI03-14, photo, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, early morning, Flying Fish Cove (intertidal), Christmas Island, coll. 9 February 2012. — 1 female, 25.2 × 15.3 (ZRC 2013.1676), Stn. CI3-15, photo-047, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, early morning, Flying Fish Cove (intertidal), Christmas Island, coll. 10 February 2012. — 1 male, 10.3 × 6.9 (ZRC 2013.1677), Stn. CI03-17, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, early morning, Flying Fish Cove (in coral rocks/rubble; infauna), Christmas Island, 11 February 2012.

Australia: 1 male, 25.3 × 17.2 (USNM 1181301), near Cairns, Green Island, Great Barrier Reef, Queensland, Australia, coll. J. Howard, 1953. — 1 male, 24.0 × 16.2 (UF 25663*), AUST-6143, HI09-035, 0–1 m, -23.4418° 151.9004°, under rock, Heron Island, Queensland, Australia, coll. CReefs Expedition, 16 November 2009. — 1 male, 20.8 × 14.1 (UF 25662*), Stn.

HI09-035, -23.4417667° 151.9004333°, 0–1 m, under rock, Heron Island, Queensland, Australia, coll. 16 November 2009. — 1 male, 21.0 × 14.0 (UF 25478*), Stn. HI09-035, -23.4417667° 151.9004333°, Heron Island, Queensland, Australia, coll. 16 November 2009. — 1 female, 32.7 × 22.2 (UF 25131*), Stn. HI09-043, -23.31741667 151.71698333, Heron Island, Queensland, Australia, coll., 17 November 2009. — 9.0 × 6.5 (UF 25520*), Stn. HI09-076, -23.4331667° 151.91708333°, 6–16 m, mostly under rocks, outer reef, Heron Island, North Heron, Queensland, Australia, coll. , 22 November 2009.

Indonesia: 1 male, 17.9 × 12.4 (ZRC 2013.1670*), Stn. BL11-010, BALI-0372, 1–2 m, under rock, coral reef, sand, sea grass, rocky shore, Sombu, Wanci, Sulawesi, Indonesia coll. 24 June 2011. — 1 female, 13.4 × 8.5 (ZRC 2013.1678), BALI-0185, Indonesia.

Malaysia: 1 male, 17.9 × 12.3 (ZRC 1965.11.11.26), Pulau Aur, Malaysia, South China Sea.

Philippines: 1 male, 14.40 × 10.50, 4 females (ZRC 2013.0735), Stn. B11, 2–4 m, 9°29.4'N 123°56.0'E, coral rubble, Pamilacan Island, coll. Panglao Expedition, 11 June 2004. — 1 male, 13.35 × 9.55, 4 females (ZRC 2013.0729*), Stn. M58, 9°31.3'N 123°41.0'E, intertidal, Balicasag Island, coll. Panglao Expedition, 4 July 2004. — 1 male, 15.25 × 10.70 (ZRC 2013.0739), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, coll. Panglao Expedition, 7 June 2004. — 1 male, 24.5 × 16.6 (USNM 65237), Basilan Strait, Little Santa Cruz Island, Zamboanga del Sur, Philippines, coll. T. Mortensen & F. Baker, 28 February 1914. — 1 male, 15.0 × 10.5 (USNM 1188422), Port Palapag, Samar Island, Northern Samar, Philippines, coll. Albatross R/V, 3 June 1909. — 1 male, 15.3 × 10.6, 1 female, 14.2 × 10.1 (USNM 154951), Balayan Bay, Luzon Island, Batangas, Philippines, coll. 27 August 1927.

Taiwan: 1 male, 8.0 × 6.1 (UF 11802*), Stn. MTAI-04, 21.95208° 120.75787°, 20–40 m, under coral, fringing reef, Tiaoshi, SE of Nanwan Bay, Kenting County, Taiwan, coll. M. Malay, 29 June 2007.

Japan: 1 male, 14.1 × 9.1 (UF 26824*), Stn. GUOK10-St-051, 26.406339° 127.844547°, 0–8 m, sheltered, shallow bay, fairly silty, Okinawa, Konbu Beach to Tengan Pier, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 29 June 2010. — 1 female, 10.6 × 7.9 (UF 26796*), Stn. GUOK10-St-051, 26.406339° 127.844547°, 0–8 m, sheltered, shallow bay, fairly silty, Okinawa, Konbu Beach to Tengan Pier, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 29 June 2010. — 1 female, 7.5 × 5.9 (UF 27002), Stn. GUOK10-St-071, 26.21218° 127.664291°, 1–8 m, silty harbor, river mouth, wharfs, Okinawa, Naha Harbor, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 16 July 2010.

Papua New Guinea: 1 male, 21.5 × 14.8 (ZRC 2013.1671), Laing Island, Papua New Guinea, coll. D. Vandenspiegel, 8 March 1992. — 4 males, 14.0 × 9.8 – 26.7 × 18.3, 1 female, 10.2 × 7.3, 2 ovigerous females, 14.6 × 10.2 – 22.8 × 15.3 (USNM 90864), near Bougainville, Puruata Island, Bismarck Archipelago, Papua New Guinea, coll. W. Necker, August 1944.

Mariana Islands: 1 female, 11.95 × 8.25 (ZRC 2000.0721), under rocks, intertidal, NW shore, Cocos Islands, Guam, coll. G. Paulay, 16 February 1998. — 1 male, 15.9 × 11.2 (USNM 1184541), 0–1 m, 13 32 54 N 144 48 24 E, hand, NCS Beach Drive, 1.7 km NE of Amantes Point, NCS Beach Drive, Tanguisson Beach, Guam, coll. R. Bolland, 14 March 1983. — 2 males, 8.2 × 5.9 – 16.9 × 11.7, 2 females, 15.4 × 10.3 – 17.6 × 12.1, 1 ovigerous female, 10.8 × 7.7, 2 juveniles, 3.7 × 2.7 – 4.2 × 3.1 (USNM 154952), coral heads, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945. — 2 males, 13.6 × 9.3 – 22.4 × 15.3, 5 females, 13.3 × 9.3 – 19.6 × 13.4 (UF 2999*), ZZZ-087497, 1–3 ft, among rocks, NE side, Alutom

Islet, Guam Islands, Mariana Islands, coll. H. Conley, 4 June 2002. — 2 females, 7.9 × 5.8 – 12.2 × 8.4 (UF 4244*), BGUAM-139, 0–1 m, under rocks, fringing reef, Rizal Beach, Guam, Mariana Islands, coll. G. Paulay, 15 July 2003. — 1 female, 9.7 × 7.0 (UF 712*), ZZZ-016529, under rocks, intertidal, NW shore, Cocos Island, Guam Island, Mariana Islands, coll. G. Paulay, 16 February 1998. — 1 male, 10.3 × 7.6, 1 female, 10.3 × 7.2, 1 damaged male (UF 1993*), ZZZ-086664, 2–4 ft, among rocks, E of Camel Rock, Hospital Point, Asan Bay, Guam Island, Mariana Islands, coll. H. Conley, 25 March 2002.

Caroline Islands: 1 male, 9.6 × 7.0, 1 female, 15.1 × 10.5 (USNM 1184842), 1 m, off southeast coast, Rock Island, Urukthapel Island, Palau, coll. R. Kropp, 28 July 1984. — 2 females, 12.5 × 8.9 – 15.8 × 10.8 (USNM 106540), 0–2 m, at W end of Ella, Elangalap Island, Ifalik Atoll, Yap Islands, Caroline Islands, Micronesia, coll. Gavileisei, 26 October 1953. — 2 males, 15.5 × 10.7 – 18.9 × 12.9 (USNM 105320), 1 02 00 N 154 45 14 E, flats next to Tipongowakarum Pass in ship, Polim Island, Kapingamarangi Atoll, Pohnpei Islands, Caroline Islands, Micronesia, coll. George Vanderbilt, 12 August 1954. — 1 male, 21.6 × 14.6 (UF 19856*), Stn. KOSR-05, 5.34222° 163.01986°, 0–0.5 m, under rocks, reef flat, Lelu, in front of Nautilus Hotel, Kosrae Island, Caroline Islands, Federated States of Micronesia, coll. S. Kim *et al.*, 29 February 2008. — 1 male, 15.1 × 10.7 (UF 14935*), Stn. KOSR-11, 5.36916° 163.01382°, 0–0.5 m, rubble on sand, under rocks, wide reef flat, seagrass, scattered live corals, Tafunsak, sandy beach in front of Nena's house, Kosrae Island, Caroline Islands, Federated States of Micronesia, coll. S. Kim *et al.*, 28 February 2008.

New Caledonia: 1 male, 11.9 × 8.5 (UF 17998*), Stn. NC09-St-5, -22.313203° 166.457452°, 1–2 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 8 March 2009. — 1 female, 15.7 × 11.5 (UF 17997), Stn. NC09-St-6, -22.313203° 166.457452°, 0–1 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 10 March 2009. — 1 male, 22.7 × 15.6 (UF 37978), NewC13-165, NEST6, -22.6503° 167.387°, 1–3 m, back reef to reef crest, Ile des Pins, New Caledonia, coll. N. Evans, 31 October 2013.

Solomon Islands: 1 male, 17.6 × 12.3 (USNM 1181371), Mohak Bay, Reef Island, Solomon Islands, coll. Templeton Crocker Expedition, 7 July 1933. — 1 male, 15.2 × 10.4, 3 females, 9.6 × 6.8 – 12.6 × 9.0 (USNM 154950), Green Island, Solomon Islands, coll. W. Bartos. — 1 male, 10.5 × 7.7 (UF 3360*), ZZZ-087897, 3–6 ft, on reef, under rocks and coral, Near Ghizo City, Ghizo Island, Solomon Islands, coll. H. Conley, 20 February 2002. — 1 male, 9.4 × 6.7 (UF 2539), Stn. ZZZ-087065, 3–20 m, among rocks and coral, Near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 13 February 2002.

Vanuatu: 1 male, 20.3 × 13.8 (ZRC 2013.1674*), Stn. DB83, 6 m, 15°43.4'S, 167°15.0'E, flat sand and dead corals, E Malo Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 03 October 2006. — 1 male, 18.4 × 12.6 (ZRC 2013.1675), Stn. DB46, photo, 2–3 m, sandy flat, 15°28.8'S, 167°15.2'E, Palikulo Bay, Vanuatu, coll. Santo Marine Biodiversity Survey, 20 September 2006.

Marshall Islands: 7 males, 7.0 × 5.0 – 21.8 × 15.2, 7 females, 8.6 × 6.2 – 15.8 × 11.0 (USNM 154977), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 male, 14.0 × 9.8 (USNM 266916), tide pools, rocky shore, lagoon side, Rigili Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. J. Garth, 21 August 1956. — 2 males, 15.8 × 11.0 – 9.8 × 7.3, 1 female, 15.2 × 10.4 (USNM 154976), Kabbenbock Island, Jaluit Atoll, Ralik Chain, Marshall Islands, coll. H. Rehder, 20 October 1960. — 4 males, 11.6 × 8.2 – 17.9 × 12.1, 7 females, 7.8 × 5.7 – 19.1 × 12.8 (USNM 154979), reef inside lagoon, Namu Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. M. Johnson, US Navy Operation Crossroads, 3 April 1946. — 1 male, 17.2 × 11.7 – 15.1 × 10.5 (USNM 154975), lagoon reef, Latoback Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. R. Bayer, 20 August 1947. — 2 males, 8.1 × 6.0 – 8.2 × 6.1, 3 females, 5.7 × 4.1 – 13.5 × 9.6 (UF 13732), Stn. FM-St-MAJ08-07, 7.14932° 171.28292°, 0–19 m, cryptofauna, patchy reefs with high coral coverage, Eneko, lagoon side, Majuro Atoll, Marshall Islands, Republic of the Marshall Islands, coll. F. Michonneau & S. Kim, 6 April 2008

Samoan Islands: 2 males, 11.8 × 8.4 – 18.2 × 12.8 (USNM 91650), outer coral reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, 1 July 1902. — 1 female, 14.8 × 10.0 (USNM 91651), coral reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, July 1902. — 1 male, 15.1 × 10.7 (UF 9549*), Stn. SMOFU-001, -14.2° -169.7°, in/on *Pocillopora damicornis*, lagoonal reef, Ofu Island, Samoa Islands, American Samoa, coll. S. McKeon, February 2007.

Kiribati and Line Islands: 2 males, 17.1 × 12.0 – 17.7 × 12.1, 3 females, 12.3 × 8.6 – 12.8 × 9.3 (USNM 154933), lagoon, Kanton Island, Kiribati, coll. C. Ely, January 1942. — 1 female, 15.7 × 10.8 (USNM 93979), about 0.5 mile offshore from central part of island, Bikati Island, Butaritari, Gilbert Islands, Kiribati, coll. P. Cloud, 3 September 1951. — 1 male, 15.6 × 10.9, 1 female, 12.8 × 9.2 (USNM 54749), Palmyra Atoll, Minor Outlying Islands, Line Islands, coll. C. Cook. — 1 female, 13.8 × 9.7 (UF 1284*), ZZZ-085757, 0.5 m, reef flat, off Captain Hook Hotel, Christmas Island, Kirimati Atoll, Line Islands, coll. C. Pittman, 22 August 1984.

Society Islands: 5 females, 16.6 × 11.4 – 20.3 × 14.0 (USNM 154937), W of Paopan Bay Entrance, Toatane Reef, Moorea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 7 May 1957. — 1 male, 23.7 × 16.0

(USNM 154938), coral, E side of entrance, Opunohu Bay, Moorea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 9 May 1957. — 1 male, 15.0 × 10.4, 2 females, 19.4 × 13.2 – 20.5 × 13.4 (USNM 154934), reef N of Taapuna Pass, Tahiti, Society Islands, French Polynesia, coll. Bredin Pacific Expedition. — 1 male, 23.1 × 16.1, 2 females, 16.7 × 11.6 – 15.0 × 10.5 (USNM 33404), between shore and fringing reef, Bora Bora, Society Islands, French Polynesia, coll. United States Fish Commission, Albatross R/V, 17 November 1899. — 6 males, 6.3 × 4.6 – 24.5 × 16.7, 5 females, 10.5 × 7.3 – 14.1 × 9.1 (USNM 154936), coral, E of Dock, Uturoa, Raiatea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 28 April 1957. — 1 male, 5.8 × 3.5 (UF 13866*), Stn. ZZZ-017503, -17.5° -149.8°, in dead *Pocillopora* head (#1), Moorea, Moorea Island, Society Islands, French Polynesia, coll. L. Plaisance, June 2006. — 1 male, 12.0 × 8.4 (UF 9847), Stn. GP-Loc-877, -17.4965° -149.8625°, 0–3 m, under rocks, fringing and patch reef at mouth of bay, Fringing Reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 male, 17.1 × 12.1 (UF 9831*), Stn. GP-Loc-877, -17.4965° -149.8625°, 0–3 m, under rocks, fringing and patch reef at mouth of bay, Fringing Reef at NW side of Opunohu Bay, Moorea Island, Society Islands, French Polynesia, coll. C. Lydeard & C. Meyer, 13 July 2006. — 1 female, 9.7 × 7.1 (UF 15710), Stn. MIB_050, -17.49631° -149.75295°, 0 m, tidal area, sand, coral, rubbles, exposed reef flat and moat, Temae reef flat, Moorea Island, Society Islands, French Polynesia, coll. J. Poupin, 9 October 2008

Tuamotu Islands: 1 male, 20.9 × 14.2, 1 female, 13.4 × 9.3 (USNM 33292), reef, Makemo Island, Tuamotu Archipelago, French Polynesia, coll. 21 Albatross R/V, October 1899. — 6 males, 7.6 × 5.4 – 17.4 × 11.7, 2 females, 10.1 × 7.2 – 14.0 × 9.6, 2 ovigerous females, 15.3 × 10.5 – 16.9 ×

11.3 (USNM 1181268), outer reef, Fakarava Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 2 October 1899. — 1 male, 11.7 × 8.3, 1 female, 11.5 × 7.9 (USNM 33295), Mohegan Reef, Rangiroa Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 23 September 1899. — 1 male, 18.5 × 12.6 (UF 1572), Stn. BTIK-001, -15.133333° -148.233333°, 0–3 m, under rocks, fringing reef and sand flat, Tuherahera Motu, lagoon fringing reef and sand flat in front to Aito Motel, Tikehau Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 10 June 2001.

Gambier Islands: 1 female, 14.9 × 10.2 (UF 35453), Stn. GAMG-49, -23.1763° -134.9023°, 18.8 m, lagoonal patch reef, Akamaru Island, Gambier Islands, French Polynesia, coll. J. Moore, 3 February 2013.

Diagnosis. Carapace (Pl. 23B) transversely hexagonal, ca. 1.5 times broad as long; dorsal surface appearing smooth without magnification, minutely granulate; regions defined by deep depressions; 2M longitudinally divided; 3M entire; medial regions well defined. Front (Pl. 23C) markedly broad; submedian lobes generally convex, joining medially to form shallow V-shaped notch, separated from lateral lobes by strong concavity. Anterolateral margin with 4 lobular teeth, sharp in young specimens, excluding outer supraorbital tooth; tooth 1 low, obtuse; tooth 2 obtuse, second largest; tooth 3 most prominent; tooth 4 small. Posterior margin shorter than anterolateral margin. Anterolateral angle of basal antennal segment entering less than halfway into orbital hiatus, flagellum free to enter orbit. Pterygostomial region granulate. Chelipeds (Pl. 23E, F) unequal, long, stout, external surfaces granulate with large protuberances; merus long, granulate, anterior margin lined with lobes, conical granules or spines; pigmentation of fixed finger extending onto inner, outer surface, and halfway length of inferior margin; dactylus long, convex; fingers gaping. Ambulatory legs (Pl. 23A) short, stout, with simple or plumose setae; extensor margin lined with short spines;

pigmented spine of dactylus longer than small subdistal spines. Male thoracic sternum (Pl. 23D) appearing smooth without magnification, minutely granulate, with sparse setae. Male abdomen (Pl. 23D) long, smooth; somite 6 longer than broad; telson longer than broad. G1 (Pl. 41D) long with numerous, simple, subdistal setae, perpendicularly and proximally directed, apex spatulate, ultimately pointed.

Remarks. Forest & Guinot (1961: 110) provided an extensive discussion on the morphological variation in *Cyclodius ungulatus*, stating that it has the greatest morphological variation among *Cyclodius* species. They also determined that the holotype of *Cyc. gracilis* Dana, 1852 is a juvenile *Cyc. ungulatus*, and synonymized the two species. Among the most misleading variations in *Cyc. ungulatus*, especially in mid-sized individuals, the carapace is sometimes smooth or granulate and the anterolateral teeth are blunt or sharp. However, as Forest and Guinot (1961) maintain, the lateral lobes of the front and shape of 2F allow straightforward differentiation between *Cyc. ungulatus* and its morphologically closest species, *Cyc. obscurus* (see remarks for *Cyc. obscurus* for further distinguishing characters). Also see remarks for *Cyc. granulatus*.

Distribution. *Cyclodius ungulatus* occurs from the Western Indian Ocean to the Hawaiian Islands and French Polynesia. It is not known from the Red Sea, Gulf of Aden, or Persian Gulf (Pl. 49C).

Luniella gen. nov.

Key to the Species of *Luniella*.

1. Anterolateral margin with 3 large anteriorly directed spines excluding outer supraorbital spine..*L. pugil*
– Anterolateral margin with 4 teeth excluding outer supraorbital tooth...2
2. G1 tip longitudinally twisted (Pl. 42C). Anterolateral angle of basal antennal segment completely or incompletely blocking orbital hiatus..*L. scabricula*
– G1 tip flattened, arched (Pl. 42A, B, D). Anterolateral angle of basal antennal segment completely blocking orbital hiatus..........................3
3. Subdistal, dorsal setae of G1 long, narrow (Pl. 42A). Absent from Western Indian Ocean...*L. pubescens*
– Subdistal dorsal setae of G1 relatively short, stout (Pl. 42D). Range restricted to Indian Ocean...*L. spinipes*

Luniella pubescens (Dana, 1852)

Pls (24, 42A, 50A)

Pilodius pubescens Dana 1852a: 80 [type locality: Balabac Strait, Philippines]; 1852b: 217 [Sulu Sea and Balabac Strait, Philippines]; 1853: 217; 1855: pl. 12, fig. 6a–d [Atlas]. — Serène 1968: 80 [List]. — Serène *et* al. 1976: 18 [Ambon, Indonesia]. — Takeda & Nunomura 1976: 62, 73 [North Island, Torres; Ile des Pins, New Caledonia]. — Dai *et al.* 1986: 307, pl. 43(6), fig. 166(3) [Review]. — Dai & Yang 1991: 331, pl. 43(6),

Fig. 166(3) [Review]. — Clark & Galil 1993: 1146, figs 12A–G, 36B, 43B [Vietnam; Ternate and Banda Neira, Indonesia; Murray I., Elizabeth Reef, North West I., Lizard I., and Wreck Reef, Australia; Touaouroo(?), Ile Ouen, Noumea, Lagune Nord, and Lagune Est, New Caledonia; Ovalau and Viti, Fiji; Samoa; Ohura; Ternae(?), French Polynesia].

Chlorodopsis pubescens Serène & Luom 1959: 316, fig. IB, 2D, 5C [Review].

Chlorodopsis melanodactylus A. Milne-Edwards 1873: 229, pl. 7, fig. 7, 7a [New Caledonia]. — Miers 1884: 531 (part). — Zehntner 1894: 151 [Ambon, Indonesia]. — Nobili 1899: 258 [Indonesia; New Caledonia; Samoa]; 1900: 498 [Indonesia; New Guinea; New Caledonia; Samoa]. — Calman 1900: 12 [Murray Island, Torres Strait]. — Ward 1932: 251 [North West Island, Australia]. — Holthuis 1953: 16 [Saipan; Onotoa, Gilbert Islands]. — Guinot 1958, fig. 23a, b.

Chlorodopsis melanodactyla De Man 1902: 624 [Ternate, Indonesia]. — Gordon 1934: 47 [Banda Neira, Indonesia]. — Serène & Luom 1958: 125, pl. ID, IIIf, IVg [Vietnam].

Chlorodopsis pilumnoides, Balss 1938a: 60 (part). (not White, 1848)

Material examined. *Australia:* 1 male, 11.6 × 7.1 (ZRC 1965.11.11.136), North West Island Capricorn Group, Australia, coll. Ward, July 1929. — 1 male, 13.7 × 8.8, 1 female, 10.4 × 6.7 (USNM 63713), outer edge of reef, North West Island, Capricorn Group, Great Barrier Reef, Queensland, Australia, coll. M. Ward, May 1930. — 1 male, 11.5 × 7.5 (UF 24669*), AUST-4613, HI09-003, 11–13 m, -23.4519° 151.8671°, by hand, in rubble, lagoon patch reefs, Wistari Reef, Heron Island, coll. S. McKeon & F. Michonneau, 11 November 2009. — 1 female (damaged) (UF 17085*), Stn. AUST-ST-050, -14.7483° 145.5165°, 0–1 m, under rocks, reef flat, S of Lizard Island, North Direction Island, Queensland, Australia, coll. A. Anker & R.

Lasley, 17 February 2009. — 1 male, 13.4 × 8.8 (UF 17084*), Stn. AUST-ST-050, -14.7483° 145.5165°, 0–1 m, under rocks, reef flat, S of Lizard Island, North Direction Island, Queensland, Australia, coll. A. Anker & R. Lasley, 17 February 2009. — 1 female, 14.0 × 8.7 (UF 24969*), Stn. HI09-025, -23.26011667° 151.91691667°, 3–6 m, in rubble, shallow patch reefs, Heron Island, Broomfield Reef, Queensland, Australia, coll. S. McKeon & F. Michonneau, 15 November 2009. — 1 female, 14.0 × 9.1 (UF 24814*), Stn. HI09-012, -23.47235° 151.9504667°, 1–2 m, in rubble, reef crest, Heron Island, Pinacle, Queensland, Australia, coll. R. Lasley, 13 November 2009.

Indonesia: 1 male, 9.9 × 6.3 (ZRC 2013.1655), Stn. BL11-015, BALI-0274, 1–3 m, hand, snorkel, under rock, coral, sand, seagrass, Sombu, Wanci, Sulawesi, Indonesia, coll. 25 June 2011. — 1 male, 10.5 × 6.8 (ZRC 2013.1656), Stn. BL11-007, BALI-0315, 8–15 m, rubble extraction, coral reef, steep slope/wall, Sombu, Wanci, Sulawesi, Indonesia, coll. 23 June 2011.

Philippines: 1 female, 9.6 × 6.3 (ZRC 2013.0740), Stn. B5, 4 m, 9°35.2'N 123°50.4'E, reef slope with overhangs, Biking, Panglao Island, coll. Panglao Expedition, 2 June 2004. — 1 female, 7.6 × 4.8 (UF 6762*), Stn. BBOL-08, 16.439667° 119.9425°, 15–30 m, fore reef, Bolinao, Left side of Mouth of Malilnep Channel, Pangasinan Province, Luzon, Philippines, coll. M. Malay, 15 July 2004.

Japan: 2 males, 7.7 × 4.9 – 13.2 × 8.6, 1 female, 10.4 × 6.7, 1 ovigerous female, 10.9 × 6.9 (ZRC 2013.1654*), Intertidal 5, Tatami-Ishi, Oh-Island, Kumejima, Okinawa, Japan, coll. 18–19 November 2009.

Caroline Islands: 2 males, 6.0 × 4.2 – 12.5 × 7.9, 2 ovigerous females, 9.5 × 6.1 – 10.5 × 6.8 (USNM 1184766), 3 m, from fore reef side, Augulpelu Reef, Palau, coll. J. Dominguez, 11 July 1984. — 1 male, 10.2 × 6.5 (USNM 1184888), PAL 79, 1 m, N side of Goraklbad Pass, S tip of barrier reef, Bablethuap Island, Palau, coll. R. Kropp, 29 July 1984. — 1 male, 8.8 × 5.6, 1 female, 9.8 × 6.5 (USNM 1184823), less than 1 m, lagoon side toward lighthouse, Ngadarak Reef, Palau, coll. R. Kropp, 16 July 1984.

Solomon Islands: 1 male, 11.2 × 7.5 (UF 2535*), ZZZ-087066, 3–6 ft, under coral heads and slabs, near JFK Island, Ghizo Island, Solomon Islands, H. Conley, 24 February 2002. — 1 male, 13.5 × 8.7 (UF 3369), ZZZ-087892, 3-6 ft, in sand, among rocks and coral, near Ghizo Island, Solomon Islands, coll. H. Conley, 17 February 2002.

New Caledonia: 1 male, 8.9 × 6.0 (UF 3429*), Stn. BNEC-001, 0.5–5 m, sand, fringing reef, Noumea, Baie de Citron, New Caledonia, New Caledonia, coll. G. Paulay, 1 January 1999. — 1 male, 12.6 × 7.8 (UF 37972), NewC13-174, NEST7, -22.5812° 167.309°, 1–2 m, fore reef, Ile des Pins, New Caledonia, coll. N. Evans, 31 October 2013..

Vanuatu: 3 males, 7.5 × 4.9 – 13.0 × 8.5, 1 female, 8.5 × 5.5, 3 ovigerous females, 8.6 × 5.5 – 10.3 × 6.7 (ZRC 2013.1657*), Stn. DB71, 7 m, 15°21.6'S, 167°12.5'E, massive coral, S Turtle Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 27 September 2006. — 1 male, 13.6 × 8.6, 2 juveniles (ZRC 2013.1658), Stn. DB29, 15 m, 15°38.9'S, 167°05.1'E, sand around coral patches, W Malo Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 17 September 2006. — 1 male, 10.3 × 6.7 (ZRC 2013.1659), Stn. DB63, 21 m, 15°26.9'S, 167°15.8'E, sand, dead and live corals, SE Aésé Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 25 September 2006. — 1 male, 9.5 × 6.3 (UF 7480), Stn. CPM-VAN-010, -15.5325° 167.2141667°, 90–100 m, reef slope, Aore Island, Aore Point, "fantastic" Dive Site, Sanma Province, Vanuatu, coll. C. Meyer, 16 January 2005.

Marshall Islands: 1 male, 9.7 × 6.8 (UF 13700*), Stn. FM-St-MAJ08-02, 7.16517° 171.03608°, 0–2 m, under rocks, reef flat, sand, sea grass bed, corals, rubble, Laura, ocean side, N end of the island, Majuro Atoll, Marshall

Islands, Republic of the Marshall Islands, coll. F. Michonneau, S. Kim, 4 April 2008.

Tonga: 1 male, 8.1 × 5.2 (USNM 134591), Eua Island, Tongatapu Group, Tonga, coll. Albatross R/V, 28 November 1899.

Samoan Islands: 1 male, 9.9 × 6.7 (UF 9539), Stn. SMOFU-001, -14.2° -169.7°, in/on *Pocillopora damicornis*, lagoonal reef, Ofu Island, Samoa Islands, American Samoa, coll. S. McKeon, February 2007.

Diagnosis. Carapace (Pl. 24B) transversely hexagonal, ca. 1.5 broad as long; surface granulate, covered in short, light-colored setae, scattered long setae; regions defined by shallow furrows, 2M, 3M entire. Front (Pl. 24C) sinuous; submedian lobes convex, separated by U-shaped notch, margin lined with conical granules; lateral lobes triangular, bearing conical granules. Anterolateral margin with 4 lobular teeth bearing anteriorly directed, pigmented spines, excluding outer supraorbital tooth; first tooth smallest, posterior three ca. equal. Posterolateral margin longer than anterolateral margin. Anterolateral angle of basal antennal segment expanded, forming flange, completely blocking orbital hiatus. Pterygostomial region minutely granulate with thick, plumose setae. Chelipeds (Pl. 24E, F) short, stout, unequal, granulate, covered with short light-colored setae, fewer long setae; merus short, anterior margin spinose; external surface of carpus and propodus with large spiniform granules; fingers of major chela short, stout, black pigmentation of fixed finger extending to outer and ventral surface of propodus; superior margin of dactyli lined with short spines, decreasing in size distally, more prominent on minor chela. Ambulatory legs (Pl. 24A) stout, setose, granulate, extensor margin lined with spines; tip of dactylus with long pigmented spine, short perpendicular subdistal spine. Male abdomen (Pl. 24D) somite 6 longer than broad; telson longer than broad. G1 (Pl. 42A) distal

1/3 curving ventrally, with row of thin, long subdistal setae; distal lobe laterally flattened, arched, curving ventrally, ultimately rounded.

Remarks. Clark & Galil (1993) reviewed the taxonomic history of *Luniella pubescens* including a discussion on its junior synonym, *Pilodius melanodactylus* A. Milne-Edwards, 1873, and brief synonymy with *Pilodius pilumnoides* (White, 1848). *Luniella pubescens* is distinguished from other *Luniella* species in having a relatively narrow carapace that is covered with short setae, a G1 with long, thin, subdistal setae, and a distribution absent from the Western Indian Ocean (Pls 24B, 42A, 50A).

Distribution. *Luniella pubescens* is recorded from the coral triangle and adjacent areas such as the Great Barrier Reef and Okinawa, Japan. It has also been collected from the western oceanic pacific islands of Tonga, Samoa and Majuro. COXI sequence data was obtained from specimens collected in Aceh, Sumatra, Indonesia. This is likely the westernmost record of the species (Pl. 50A).

Luniella pugil (Dana, 1852)

Pls (25, 42B, 50B)

Pilodius pugil Dana 1852a: 80 [type locality: Samoa; also Balabac Strait, Philippines]; 1852b: 219 [Upolu, Samoa; Balabac Strait, Philippines]; 1853: 219 [Review]; 1855: pl. 12, fig. 8a–l [Atlas]. — Heller 1865: 19 [Nicobar]. — ?Laurie 1906: 406 [Gulf of Manaar]. — Forest & Guinot 1961: 91 [Hikueru, Tuamotu Islands; Mangariva, Gambier Islands]. — Guinot 1964b: 67 [Abulat, Saudi Arabia]; 1967: 268. — Serène 1968: 80 [List]. — Sakai 1976: 462, pl. 164, fig. 4 [Yoron I. and Ishigaki I., Japan]. Serène *et al*. 1976: 18 [Ambon I., Indonesia]. — Peyrot-Clausade 1977a:

27 [Tulear, Madagascar]; 1977b: 213 [Moorea]; 1989: 113 [Tikehau, Tuamotu]. — Chen & Lan 1978: 267 pl. 4, fig. 14 [Xisha Islands]. — Serène 1984: 242, figs 143f, 147, pl. XXXIIIF [Tamatave, Madagascar; Ile Aldabra; Mayotte, Comoros Islands; Ile Maurice]. — George & George 1987: 238 (list). Table 5. — Dai *et al.* 1986: 308, pl. 44(1), fig. 166(4) [Review]. — Dai & Yang, 1991: 332, pl. 44(1), fig. 166(4) [Review]. — Clark & Galil 1993: 1149, figs 13A–G, 37A, 43C [Abulat I., Saudi Arabia; Aldabra; Mayotte; Tamatave, Madagascar; Mauritius; Reunion; Egmont Reef and Salomon, Chagos; Hulhule, Maldives; Minikoi, Laccadive Is.; Funafuti, Ellice Is.; Gulf of Mannar; Ishigaki I., Japan; Phuket, Thailand; Pulau Mantabuan, Philippines; Ternate and Ambon, Indonesia; Murray I., North West Islet, One Tree I., and Swain Reef, Australia; Grand Recif Sud, New Caledonia; Gilbert I.; Samoa; Lagoon de Has(?); Moorea; Takapoto and Hikueru, Tuamotu Is.].

Chlorodopsis pugil Nobili 1907: 395 [Mangareva I., Gambier Is.]. — Gordon 1934: 48 [Banda Neira, Indonesia]. — Ramadan 1936: 33 (part) [Ghardaqa, Egypt, Red Sea]. — Balss 1938a: 61 [Aranuka and Tapitoea, Gilbert Islands; Viti Levu and Namuka, Fiji Island; Ebon, Marshall Islands; Samoa; Madagascar]. — Sakai 1939: 506 [Loo Choo and Yaeyama, Japan]. — Ward 1939: 10 [Savaii Island, Samoa]. — Miyake 1939: 216 [List]. — Lin 1949: 23 [Taiwan]. — Holthuis 1953: 17 [Saipan; Onotoa, Gilbert Islands]. — Sakai 1956: 40 [Appendix]. — Guinot 1958a: 180 [Mayotte]; 1967c: 268 [List]. — Serène & Luom 1959: 319, figs 2K, 3A, 5D, pl. II, fig. c, pl. III, figs D, D' [Vietnam]. — Chen & Lan 1978: 267, pl. 4, fig. 14 [Xisha].

Chlorodopsis spinipes, A. Milne-Edwards 1873: 230 pl. 8, fig. b [New Caledonia]. — De Man 1887b: 282 [Ambon I., Indonesia]; 1892: 278; 1902: 626 [Ternate, Indonesia]. — Ortmann 1893: 471 [Amami Oshima, Japan; Samoan Is.]. — Henderson 1893: 361 [Sri Lanka; Muttuwartu Par, India]. — Zehntner 1894: 151 [Ambon I., Indonesia]. — Alcock 1898: 169 [Andaman Islands, India; Mergui Archipelago, Myanmar]. — Calman 1900: 12 [Murray I., Torres Strait]. — Borradaile 1900: 588 [Funafuti]; 1902: 261 [Male and Minikoi atolls, Lakshadweep].— Rathbun 1907: 50, pl. 2, fig. 5 [Rangiroa I.; Fakarava I.; Makemo I.; Bora Bora I.; Funafuti]; 1911: 226 [Salomon, Egmont Reef, Diego Garcia, Coetivy].. — Lenz 1910: 551 [Madagascar]. — Ward 1932: 251 [North West Island, Australia]. — Miyake 1936: 509 [Yaeyama, Japan]. — Serène & Luom 1958: 135; pl. 1, fig. 13, pl. 4, fig. h. — Sankarankutty 1961: 121 [List], 129. — Michel 1964: 24 [Mauritius]. [not *Luniella spinipes* (Heller, 1861)]

Pilumnus globosus Boone 1934: 152, pl. 78 [Tahiti].

Material examined. *Seychelles:* 1 male, 11.5 × 7.1 (USNM 41261), Coetivy Island, Seychelles, coll. J. Gardiner, Sealark Expedition, Sealark R/V, 1905.

Mascarene Islands: 1 male, 10.6 × 6.7 (UF 12558*) BREU-FM-0044-1, SWIO-FM29, 0–2 m, -21.0941° 55.2347°, Planch'Alizé, La Saline, Reunion Island, Mascarene Islands, coll. N. Hubert & F. Michonneau, 20 July 2007. — 1 male, 11.2 × 7.3 (UF 12850*), BREU-1259, SWIO-22, 0–2 m, -21.0956° 55.2336°, rotenone, in rubble, fringing reef moat, Planch'Alizé, La Saline, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al*., 16 August 2007. — 1 male, 7.3 × 4.7 (UF 12643*), Stn. SWIO-2, -21.107222° 55.248889°, 0–1 m, on *Acropora*, fringing reef moat, Saint-Paul, Varangue du lagon, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al.*, 6 August 2007.

Chagos Islands: 1 male, 12.8 × 8.2, 1 female, 9.5 × 6.4 (USNM 41262), lagoon, Diego Garcia Atoll, Chagos Archipelago, British Ocean Territory, coll. J. Gardner, Sealark Expedition, 8 July 1905.

Maldives: 2 males, 8.2 × 5.3 – 10.1 × 6.6 (ZRC 2007.0739), Laamu Atoll, Maldives, coll. A. Kumar, November 2007.

Thailand: 5 males, 7.7 × 4.9 – 13.1 × 8.4 (ZRC 1970.3.13.8-13), Phuket, Thailand, coll. R. Serène, 4 February 1966. — 2 males, 9.1 × 5.9 – 10.2 × 6.6, 3 females, 7.4 × 4.8 – 10.8 × 6.9, 1 ovigerous female, 7.7 × 5.1 (USNM 184263), Marsden Square: 027, Phuket Island, Thailand, Andaman Sea, coll. Fifth Thai Danish Expedition, Gallardo R/V, 4 February 1966.

Australia: 1 male, 9.4 × 6.2 (UF 25532*), AUST-5945, HI09-077, 2–4 m, -23.445° 151.9504°, bommies on sand, Heron Lagoon, Heron Island, Queensland, Australia, coll. 22 November 2009. — 1 female, 11.9 × 7.4 (UF 17095*), 0 m, North Direction Island, S of Lizard Island, Queensland, Australia, coll. A. Anker & R. Lasley, 17 February 2009.

Philippines: 1 female, 11.04 x 6.76 (AMNH 18503), Padada Beach, Gulf of Davao, Philippines, coll. G. Oesch, September 1939. — 1 male, 9.55 × 6.35, 1 female (ZRC 2013.0730), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, Panglao Expedition 2004, coll. 7 June 2004. — 1 male, 7.4 × 4.7 (ZRC 2013.0744), Stn. S15, 5–12 m, 9°29.3'N 123°55.1'E, fringing reef, Pamilacan Island, 15 June 2004. — 1 male, 11.50 × 7.30 (ZRC 2013.0728), Stn. B34, 1–2 m, 9°38.3'N 123°50.3'E, channel between inlet and the open sea, Sungcolan inlet, Panglao Island, coll. Panglao Expedition, 28 June 2004.

Mariana Islands: 1 male, 6.7 × 4.6 (UF 2955*), 2 m, N and NE side, Alutom Islet, Guam Island, Mariana Islands, coll. H. Conley, 10 June 2002. — 1 female, 7.3 × 4.5 (UF 2839*), 1 m, Asan Point, Guam, Mariana Islands, coll. H. Conley, 3 July 2002. — 1 male, 8.3 × 5.1 (USNM 65279), Apra Bay, Guam, coll. Albatross Philippines Expedition, Albatross R/V, 20 November 1907. — 1 male, 10.6 × 6.5, 4 females, 4.9 × 3.3 – 8.0 × 5.1 (USNM 1184916), 0–1 m, outer reef platform, Tumon Bay, Guam, coll. J. Dominguez, 23 March 1984. — 2 males, 4.8 × 3.4 – 8.2 × 5.2, 1 ovigerous female, 8.5 × 5.3 (USNM 1181395), in coral, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945. — 2 males, 8.2 × 5.4 – 9.6 × 6.1, 2 females, 5.2 × 3.4 – 6.9 × 4.5, 4 ovigerous females, 6.2 × 4.0 – 8.7 × 5.5 (USNM 1181412), in coral, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945.

Caroline Islands: 2 males, 7.4 × 5.0 – 10.6 × 7.0, 1 ovigerous female, 9.6 × 6.1 (USNM 1184836), 2 m, facing Malkal (Malakal) Pass, large patch reef in bay along NE coast of island, Urukthapel Island, Palau, coll. J. Dominguez, 5 July 1984. — 1 male, 8.7 × 5.8 (USNM 1184847), 1 m, off SE coast, Rock Island, Urukthapel Island, Palau, coll. R. Kropp, 28 July 1984. — 1 male, 9.4 × 5.9, 1 female, 4.6 × 2.9 (USNM 1184891), 1.7 m, facing Malakal Pass, patch reef in large bay on NE coast, Urukthapel Island, Palau, coll. R. Kropp, 20 July 1984. — 1 female, 8.5 × 5.3 (USNM1181202), 1–2 m, NW of Nikalap Aru Islands, Ant Atoll, Pohnpei Island, Pohnpei Islands, Caroline Islands, Micronesia, coll. R. Kropp, Birkeland, 17 November 1984. — 1 female, 10.6 × 7.0 (USNM 106706), lagoon reefs at Ketalu, Ifalik Atoll, Yap Islands, Caroline Islands, Micronesia, coll. F. Bayer, 30 October 1953. — 1 male, 11.2 × 7.0, 1 female, 10.6 × 6.7 (USNM 106705), lagoon reef opposite Fan-Nap and Rolong Canoe-House, Rauau, Falarik Island, Ifalik Atoll, Yap Islands, Caroline Islands, Micronesia, coll. Fourth Pacific Atoll Survey, coll. 24 September 1953. — 1 male, 10.8 × 6.7 (UF 5280), Stn. JAS-PON-070, 6.99° 158.23°, 2–3 m, under rock, reef flat, Lenger Island, Next to Japanese Dock at Clam Hatchery, Pohnpei Island, Caroline Islands, Federated States of Micronesia, coll. J. Starmer, 13 March 2003.

Solomon Islands: 1 male, 9.7 × 6.1 (UF 3196*), ZZZ-087843, 3-5 ft, under rocks and coral heads, near JFK island, Ghizo Island, Solomon Islands, coll. H. Conley, 19 February 2002. — 1 male, 8.4 × 5.4 (UF 3400), ZZZ-087900, 3–5 ft, among dead coral and rocks, Near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 10 February 2002.

New Caledonia: 1 male, 13.0 × 8.3 (UF 3430*), BNEC-001, GP 547:32–34, 0.5–5 m, sand, fringing reef, Baie de Citron, Noumea, New Caledonia, coll. G. Paulay, 1 January 1999. — 1 female, 6.8 × 4.6 (UF 37968*), NEST3, -22.6681° 167.425°, 1–3 m, coral rubble, coralline algae, Ile des Pins, New Caledonia, coll. N. Evans, 29 October 2013.

Vanuatu: 1 male, 8.4 × 5.0 (ZRC 2013.1660), Stn. DB67, photo, 7 m, 15°22.9'S, 167°13.1'E, sand and dead corals, W Mavéa Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 26 September 2006. — 2 females, 7.6 × 4.7 – 7.8 × 5.0 (ZRC 2013.1661), Stn. DB53, 5 m, 15°28.8'S, 167°15.2'E, dead corals, Palikulo Bay, Vanuatu, coll. Santo Marine Biodiversity Survey, 22 September 2006.

Marshall Islands: 1 male, 8.6 × 5.5 (UF 29675*), lagoon side, Eneko, Majuro Atoll, Marshall Islands, coll. F. Michonneau & S. Kim, 6 April 2008. — 1 male, 11.5 × 7.2 (USNM 266914), ocean side, Parry Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. D. Reish, 21 August 1956. — 1 male, 9.8 × 6.2, 3 females, 5.2 × 3.4 – 7.7 × 4.9 (USNM 134598), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt, June 1950. — 2 females, 4.7 × 3.2 – 9.0 × 5.4 (USNM 1181394), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 female, 8.9 × 5.6 (USNM 1181427), poison + seine, reef at shore inside lagoon, Namu Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. J. Morrison, 3 April 1946. — 4 males, 6.1 × 4.0 – 11.2 × 7.2, 6 females, 7.1 × 4.6 – 10.3 × 6.6 (USNM 1181398), poison + seine, reef at shore inside lagoon, Namu Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. J.

Morrison, 3 April 1946. — 3 males, 8.7 × 5.4 – 10.8 × 6.6, 1 female, 9.7 × 6.2 (USNM 1181409), Bogen Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. H. Ladd, 1952. — 1 damaged male (USNM 1181401), lagoon reef, Latoback Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. R. Bayer & F. Zimmerman, 21 August 1947. — 3 males, 7.7 × 5.1 – 11.9 × 7.6, 2 females, 6.2 × 4.1 – 8.6 × 5.5 (USNM 1181411), Kabbenbock Island, Jaluit Atoll, Ralik Chain, Marshall Islands, coll. H. Rehder, 20 October 1960.

Tuvalu: 2 females, 9.0 × 5.8 – 10.1 × 6.2 (USNM 33310), Ellice Island, Funafuti Atoll, Tuvalu, coll. Albatross R/V, 24 December 1899.

Tonga: 1 male, 6.2 × 4.0 (USNM 1181432), Eua Island, Tongatapu Group, Tonga, coll. Albatross R/V, 28 November 1899.

Samoan Islands: 1 male, 11.2 × 6.9 (USNM 1181402), outer reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, 27 June 1902. — 1 male, 8.4 × 5.3 (USNM 1181426), mouth of river, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, June 1902. — 1 male, 5.9 × 3.8, 1 female, 7.2 × 4.6 (USNM 1181418), Pago Pago, Tutuila Island, American Samoa, coll. United States Fish Commission, August 1902.

Kiribati: 1 male, 9.7 × 6.4, 1 female, 8.7 × 5.6 (USNM 95081), Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 8 August 1951. — 1 male, 10.1 × 6.6, 1 female, 7.6 × 4.9 (UF 1282*), 0.5 m, off Captain Hook Hotel, Christmas Island, Kiritimati Atoll, Line Islands, Kiribati, coll. C. Pittman, 22 August 1984. — 1 female, 8.5 × 5.4 (USNM 93965), 0–0.3 m, 1300 ft NE of Namokora, Onotoa Atoll, Gilbert Islands, Kiribati, coll. P. Cloud, 21 August 1951.

Society Islands: 1 female, 10.3 × 6.7 (UF 10267), BMOO-323, zzzMoorea-137, -17.4747° -149.8128°, Price's settling plates from CTD-1, ex Nicole, Moorea Island, Society Islands, coll. N. Price. — 1 female, 9.2 × 6.0 (UF 18048*). — 1 male, 8.7 × 5.5 (UF 9877*), BMOO-1102, GP-Loc-878, 0–2 m, -17.4982° -149.8636°, by hand, fringing and patch reef at mouth of bay, within reef rock rubble, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, coll. C. Lydeard *et al*., 13 July 2006. — 3 males, 6.5 × 4.5 – 11.2 × 7.2, 5 females, 7.6 × 4.7 – 11.8 × 7.6 (USNM 33412), fringing reef, Bora Bora, Society Islands, French Polynesia, coll. Albatross R/V, 17 November 1899. — 1 female, 8.6 × 5.8 (USNM 1181415), near Pahua Point in coral, Bora Bora, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 23 April 1957. — 1 female, 7.2 × 4.8, 1 ovigerous female, 10.3 × 6.7 (USNM 1181397), head of Baie de Maroe, Huahine, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 30 April 1957. — 1 male, 10.9 × 7.0 (USNM 1181419), Bourayne Bay, Huahine, Society Islands, French Polynesia, 1 May 1957. — 2 males, 6.1 × 4.0 – 10.9 × 7.1, 2 females, 5.1 × 3.7 – 8.2 × 5.3 (USNM 1181431), E of dock, Uturoa, Raiatea, Society Islands, French Polynesia, coll. 28 April 1957. — 3 males, 9.10 × 5.8 – 11.5 × 7.2, 1 female, 10.4 × 6.6, 1 damaged juvenile (USNM 1181410), 1 m, reef N of Taapuna Pass, Punaaula District, Tahiti, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 21 April 1957.

Tuamotu Islands: 1 female, 10.4 × 6.5 (USNM 1181267), shore, Lagoon Cove, Maiai Island, Tikehau Atoll, Tuamotu Archipelago, French Polynesia, coll. Bredin Pacific Expedition, 13 April 1957. — 4 males, 4.5 × 3.1 – 8.2 × 5.5, 6 females, 4.1 × 2.8 – 11.4 × 7.3, 6 juveniles (USNM 1181424), lagoon, Tikehau Atoll, Tuamotu Archipelago, French Polynesia, coll. Bredin Pacific Expedition, 11 April 1957. — 1 female, 5.3 × 3.4, 1 ovigerous female, 10.2 × 6.6 (USNM 33309), outer reef, Fakarava Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 12 October 1899. — 1 male, 9.6 × 6.2 (USNM 33308), Mohegan Reef, Rangiroa Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 23 September 1899. — 2 females, 9.0 × 5.7 – 10.0 × 6.4 (USNM 33307), reef, Makemo Island, Tuamotu

Archipelago, French Polynesia, coll. Albatross R/V, 21 October 1899. — 1 male, 7.8 × 5.1 (UF 30321), Stn. BTIK-001, -15.133333° -148.233333°, 0–3 m, under rocks, fringing reef and sand flat, Tuherahera Motu, lagoon fringing reef and sand flat in front to Aito Motel, Tikehau Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 10 June 2001. — 1 male, 7.4 × 4.9 (UF 35307), Stn. HAO-003, -18.06897° -140.984929°, 0.5–3 m, fringing reef and back reef, Hao Atoll, near red channel marker, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 18 January 2013. — 1 ovigerous female, 11.5 × 7.3 (UF 35305), Stn. HAO-003, -18.06897° -140.984929°, 0.5–3 m, fringing reef and back reef, Hao Atoll, near red channel marker, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 18 January 2013.

Gambier Islands: 1 female, 6.4 × 4.2 (UF 35494*), Stn. GAMBIER-3, -23.15174° -135.05536°, 0.5–9 m, muddy lagoon, Terevai Island, in small bay, Gambier Islands, French Polynesia, coll. J. Moore & C. Payri, 8 February 2013.

Diagnosis. Carapace (Pl. 25B) transversely hexagonal, ca. 1.6 broad as long; surface granulate, appearing smooth without magnification; regions well-defined; 2M entire, anterior margin with cluster of ca. 3 long setae, 3M entire. Frontal (Pl. 25C) submedian lobes angular, separated by wide, deep U- or V-shaped notch, mesially transverse, laterally diagonal, margin granulate; lateral lobes triangular. Anterolateral margin with 3 large anteriorly directed, spines excluding outer supraorbital spine. Anterolateral angle of basal antennal segment expanded, completely blocking orbital hiatus. Pterygostomial region minutely granulate with thick, plumose setae. Chelipeds (Pl. 25E, F) unequal; merus stout, anterior margin with long spines; external surface of carpus and propodus prominently spinose, spines stout; fingers of major chela short, stout, dark, pigmentation of propodus restricted to fixed finger; superior margin of dactyli lined with short spines, decreasing in size distally, few proximal spines on major chela, more prominent on minor chela. Ambulatory legs (Pl. 25A) stout, extensor margin lined with long, thick, plumose and simple setae; tip of dactylus with long pigmented spine, short perpendicular subdistal spine. Male abdomen (Pl. 25D) long; somite 6 ca. broad as long; telson longer than broad. G1 (Pl. 42B) distal 1/3 curving ventrally, with cluster of proximally-directed subdistal setae; distal lobe laterally flattened, arched, curving ventrally, ultimately rounded.

Remarks. *Luniella pugil* differs from other species in having an anterolateral margin with only 3 teeth (the first is reduced and ventral in position, or obsolete), which are long, anteriorly directed spines without accompanying granules or spines nearby (Pl. 25B). The carapace is also adorned with lateral, robust, conical granules or spines, and the carpus and propodus of the chelipeds are covered with long sharp spines and granules (Pl. 25A). *Luniella pugil* has often been confused with the variable species, *L. spinipes*. Some *L. spinipes* specimens have anterolateral and cheliped spines similar to those of *L. pugil*. However, these spines in *P. pugil* are conspicuously longer. The first anterolateral tooth is also much more reduced in *P. pugil*, even compared to particularly spinose *P. spinipes* specimens. Furthermore, the G1s of these species are very similar (Pl. 42B, D). However, the G1 of *L. pugil* has an apical lobe that is relatively broader, and the subdistal, ventral surface is spinose (versus relatively narrow with stout setae on the subdistal, ventral surface).

Distribution. *Pilodius pugil* has a widespread IWP distribution from the Western Indian Ocean to French Polynesia. It has not known from the Hawaiian Islands (Pl. 50B).

Luniella scabricula (Dana, 1852)

Pls (26, 42C, 50C)

Pilodius scabriculus Dana 1852a: 80 [type locality: Balabac Strait, Philippines; also Raraka Atoll, Tuamotu Islands]; 1852b: 220 [Balabac Strait, Philippines]; 1853: 220 [List]; 1855, pl. 12, fig. 9 [Atlas]. — Nobili 1907: 394 [Marutea Sud, Fakarava, and Fakahina, Tuamotu Archipelago; Temoe, Gambier Islands]. — Guinot 1962: 6 [Europa I.]; 1967c: 268 [List]. — Forest & Guinot 1961: 91, fig. 83a, b, fig. 84, 86 [Hikueru, Tuamotu Islands; Tahiti]. — Serène 1968: 80 [List]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]; 1977b: 213 [Moorea]; 1989: 113 [Tikehau, Tuamotu]. — Thomassin 1978: 64 (Appendix 3) [Tulear, Madagascar]. — Serène 1984: 244, fig 143 i, 149, pl. XXXIV [Nosy Fany, Madagascar; Iles Glorieuses; Ile Europa]. — Dai *et al.* 1986: 309, pl. 44(2), fig. 166(5) [Review]. — Dai & Yang 1991: 332, pl. 44(2), fig. 166(5) [Review]. — Clark & Galil 1993: 1152, figs 14A–G, 37B, 43D [Glorioso Is.; Europa I.; Nosy Fany, Madagascar; Coin Peros, Chagos; Coetivy, Seychelles; Cocos Keeling I.; Christmas I.; (13 mi SE of) Cape Capricorn, Wreck Reef (near Porpoise Cay), and Green I., Australia; Yap I. and Ifaluk Atoll, Caroline Is.; Huanine I.; Saipan I.; Arno Atoll; Eniwetok Atoll; Canton I.; Bikini Atoll; Namu I.; Enurikku I.(?); Moorea; Bora Bora; Raiatea; Vaiorea I.; Palmyra; Temoe(?); Fakahina; Hao I.; Tahiti; Hikueru; Marutea; Tickahau, Atoll; Maiai I.].

Chlorodopsis venusta Rathbun 1907: 49, pl. 1, fig. 5 [Fakarava I. and Makemo, Tuamotu Is.; Funafuti]; 1911: 226 [Salomon, Egmont, Peros, Coetivy]. — Calman 1909: 705 [Christmas Island]. — Ward, 1941: 11 [List]. — Tweedie 1947: 27 [List]. — Serène & Luom 1958: 131, pl. II, fig. C, pl. III fig. e, pl. IV, fig. f [Vietnam]; 1959: 317, figs 2 N, 5 H [Review].

Chlorodopsis scabriculus ?Rathbun 1911: 226 [Coetivy]; Edmondson 1923a: 17 [Palmyra I.; Fanning I.]; 1925: 43 [Wake I]; 1933: 250 [Review]. — Ward 1932: 250–251 [North West Island, Australia]. — ?Edmondson 1933: 250 [Review].

Chlorodiella venusta Balss 1938a: 53 (part) [Oceanic Pacific].

Chlorodopsis melanodactylus, Tweedie 1950b: 121, pl. XVII d, e [Cocos-Keeling Islands]. (not *Pilodius melanodactylus* A. Milne-Edwards, 1873)

Chlorodopsis spinipes, Sankarankutty 1962: 139, fig. 40, 41 [S Andaman, India]. (not *Pilodius spinipes* Heller, 1861)

Chlorodopsis pilumnoides, Garth 1964: 140 [List]. [not *Pilodius pilumnoides* (White, 1848)]

Chlorodopsis natalis Serène, 1984, p. 233 *nomen nudem*.

(?) *Pilodius pugil*, Peyrot-Clausade, 1989: 112 [Tikehau, Tuamotu]. (not *Pilodius pugil* Dana, 1852)

Material examined. *Seychelles:* 2 males, 9.7 × 6.2 – 12.5 × 7.6, 2 females, 5.9 × 3.7 – 10.5 × 6.5 (USNM 41267), Coetivy Island, Seychelles, coll. J. Gardiner, Sealark Expedition, Sealark R/V, 1905.

Chagos Islands: 1 male, 8.1 × 5.1, 1 ovigerous female, 6.3 × 4.1 (USNM 41266), Egmont Reef, Chagos Archipelago, British Indian Ocean Territory, coll. J. Gardiner, Sealark Expedition, Sealark R/V, 1905.

Maldives: 1 male, 10.1 × 6.2 (ZRC 2007.0741), Laamu Atoll, Maldives, coll. A. Kumar, November 2007.

Christmas Island: 1 male, 11.1 × 7.0 (ZRC 2013.1663), Stn. CI3-15, photo-056, S10.429863 E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, Flying Fish Cove (intertidal), Christmas Island, coll. 10 February 2010. — 4 males, 6.3 × 4.0 – 10.8 × 6.6, 6 females, 5.2 × 3.5 – 8.8 × 5.4 (ZRC 2013.1664*), Stn. CI03-17, S10.429863

E105.667135, coralline rocks, large boulders, mixed with coral rubble and sand, few live corals, Flying Fish Cove (in coral rocks/rubble; infauna), Christmas Island, coll. 11 February 2012. — 3 males, 8.4 × 5.3 – 10.3 × 6.6 (ZRC 2013.1665), Stn. CK2, Christmas Island.

Australia: 1 male, 7.5 × 4.6 (USNM 156078), Green Island, Great Barrier Reef, Queensland, Australia, coll. W. Bartos.

Japan: 4 males, 7.0 × 4.2 – 9.1 × 5.8 (ZRC 2013.1662*), Intertidal 5, Tatami-Ishi, Oh-Island, Kumejima, Okinawa, Japan, coll. 18–19 November 2009.

Mariana Islands: 1 male, 8.7 × 5.2 (UF 15071*), ZZZ-087497, 1–3 ft, among rocks, NE side, Alutom Island, Guam Island, Mariana Islands, coll. H. Conley, 4 June 2002. — 1 male, 5.6 × 3.5 (USNM 1184964), 1.2 m, mid moat, reef flat off Fujita Hotel, Tumon Bay, Guam, coll. J. Dominguez, 23 May 1984. — 1 male, 7.9 × 5.0 (USNM 1184913), 0–1 m, outer reef platform, Tumon Bay, Guam, coll. J. Dominguez, 23 March 1984. — 4 males, 6.2 × 3.9 – 7.7 × 4.9, 2 females, 7.0 × 4.3 – 7.8 × 4.9, 1 ovigerous female, 5.9 × 3.7 (USNM 1181437), in coral heads, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945. — 1 male, 7.5 × 4.7 (USNM 1181457), in coral heads, Saipan Island, Northern Mariana Islands, A. Banner, 1945. — 2 males, 5.4 × 3.4 – 7.8 × 4.9, 1 female, 5.2 × 3.2 (UF 5658), Stn. ZZZ-090333, 13.5° 144.8°, rubble, Double Reef, Guam Island, Mariana Islands, USA, coll. L. Kirkendale, 8 May 2002.

Caroline Islands: 1 male, 4.7 × 3.0 (USNM 1181465), 0.2 m, transect D, about halfway between breakers and lagoon reef margin, western reef between Elangalap Island and the N end of Falarik Island, Ifalik Atoll, Yap, Caroline Islands, Micronesia, coll. D. Abbott, Yaniseman, Pacific Science Board Survey, 21 September 1953. — 1 male, 5.7 × 3.6 (USNM 156077), Yap Island, Yap Islands, Caroline Islands, coll. R. Hiatt.

Marshall Islands: 1 male, 9.0 × 5.8 (USNM 1181460), outer reef, Enyu Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. F. Bayer, 1 August 1947. — 1 male, 7.7 × 4.9, 1 female, 9.1 × 5.6 (USNM 1181440), reef inside lagoon, Namu Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. M. Johnson, US Navy Operation Crossroads, 3 April 1946. — 2 males, 8.9 × 5.5 – 9.9 × 6.1, 3 females, 6.9 × 4.5 – 8.9 × 5.6 (USNM 1181458), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 male, 9.0 × 5.1 (USNM 1181455), East Rigili Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. J. Morrison, 30 May 1946. — 2 males, 5.0 × 3.2 – 5.6 × 3.5, 1 female, 7.7 × 4.9 (USNM 134597), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt, June 1950. — 1 male, 8.5 × 5.4, 1 female, 7.4 × 4.6 (USNM 134596), lagoon, Rigili Island, Enewetak Atoll, Ralik Chain, Marshall Islands, H. Ladd, May 1952.

Samoan Islands: (?)1 female, 4.6 × 3.0 (UF 9527), Stn. SMOFU-001, -14.2° -169.7°, in/on *Pocillopora damicornis*, lagoonal reef, Ofu Island, Samoa Islands, American Samoa, coll. S. McKeon, February 2007. — ?1 male, 6.4 × 4.1 (UF 3288), Stn. VB-028a, 3–15 m, under rocks and crevices, Tutuila Island, Samoa Islands, American Samoa, coll. V. Bonito, 28 October 2002.

Cook Islands: 1 male, 6.3 × 4.2 (UF 11714*), Stn. MRARO-001, -21.233333° -159.766667°, 0–5 m, reef flat, Vaima'anga (S Coast) near Captain Cook Resort, in front of Teina's brother's house, Rarotonga Island, Cook Islands, Cook Islands, coll. M. Malay, 23 June 2006.

Society Islands: 1 male, 9.2 × 5.7 (UF 9890*), BMOO-01141, GP-Loc-878, 0–2 m, -17.4982° -149.8636°, fringing and patch reef, fringing reef at NW side of Opunohu Bay, Moorea Island, Society Islands, coll. C. Lydeard, C. Meyer, 13 July 2006. — 2 males, 6.5 × 4.1 – 6.5 × 4.3, 1 female, 7.1 × 4.4 (USNM 1181439), lagoon side of ocean reef, W of Motu Tapu, Bora Bora, Society Islands, French Polynesia, coll. W. Schmitt, 25 April 1957. — 4 males, 4.7 × 3.1 – 7.5 × 4.7, 4 females, 7.1 × 4.4 – 8.6 × 5.4 (USNM 1181438), lagoon side of ocean reef, W of Motu Tapu, Bora Bora, Society Islands, French Polynesia, coll. W. Schmitt, Bredin Pacific Expedition, 25 April 1957. — 11 males, 4.1 × 2.7 – 8.9 × 5.5, 8 females, 4.4 × 3.0 – 5.9 × 3.8, 6 ovigerous females, 6.0 × 4.0 – 8.1 × 5.3, 3 juveniles (USNM 1181456), reef, N of Baie Fare and S of Point Teopape, off Point Teffaar, Huahine, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 2 May 1957. — 1 male, 9.3 × 5.8, 4 females, 3.5 × 2.5 – 6.0 × 3.8, 2 ovigerous females, 5.7 × 3.6 – 7.7 × 4.7, 3 juveniles (USNM 1181462), Moorea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 9-10 May 1957.

Kiribati: 1 male, 9.0 × 5.7 (UF 10513*), sand spit on S end of main reef passage, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay, 7 August 2005. — 2 males, 6.2 × 4.0 – 7.7 × 4.9, 1 female, 6.3 × 4.1 (USNM 94020), Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 26 July 1951. — 2 males, 5.4 × 3.5 – 5.7 × 3.7, 1 female, 7.2 × 4.6, 1 ovigerous female, 6.5 × 4.3 (USNM 94021), Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 8 August 1951.

Tuamotu Islands: 1 male, 9.0 × 5.6 (UF 31176), BRNG-032, -14.9833° -147.6167°, nestled in, outer reef flat and reef crest, off far W Hoa, Avatoru Motu, Rangiroa Atoll, Tuamotu Islands, coll. G. Paulay, 26 October 2001. — 1 male, 10.9 × 7.1 (UF 1614*), BTIK-001, 0–3 m, -15.1333° -148.2333°, under rocks, lagoon fringing reef and sand flat in front of Aito Motel, Tuherahera Motu, Tikehau Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 10 June 2001. — 1 female, 9.5 × 5.9 (UF 1546), BRNG-032, -14.9833° -147.6167°, nestled in, outer reef flat, and reef crest, off far W Hoa, Avatoru Motu, Rangiroa Atoll, Tuamutu Islands, French Polynesia, G. Paulay, 30 October 2001. — 3 male, 6.2 × 3.8 – 8.2 × 4.9 (USNM 33327), outer reef, Fakarava Island, Tuamotu Archipelago, French Polynesia, coll. Albatross R/V, 12 October 1899. — 1 male, 8.5 × 5.2, 2 females, 9.3 × 5.9 – 9.4 × 5.7 (UF

1595*), Stn. BRNG-032, -14.98333° -147.61667°, nestled in crevices in reef rock, outer reef flat, and reef crest, Avatoru Motu, off Far W Hoa, Rangiroa Atoll, Tuamotu Islands, French Polynesia, coll. G. Paulay, 26 October 2001.

Pitcairn Islands: 1 ovigerous female, 9.9 × 6.0 (UF 2619), Stn. ZZZ-087242, Ducie Atoll, Pitcairn Islands, Pitcairn Islands, coll. G. Wragg, P. Marriott, 6 November 1997.

Diagnosis. Carapace (Pl. 26B) transversely hexagonal, ca. 1.6 broad as long; surface granulate, shagreened, with few or no setae; regions defined; 2M, 3M entire. Frontal (Pl. 26C) submedian lobes convex, sometimes straight, separated by shallow V-shape notch, margin granulate; lateral lobes triangular. Anterolateral margin with 4 teeth; tooth 1 small, sometimes difficult to distinguish from surrounding granules; teeth 2–3 larger, with anteriorly directed apical spines. Anterolateral angle of basal antennal segment expanded, completely or incompletely blocking orbital hiatus. Pterygostomial region minutely granulate, covered with thick, plumose setae. Chelipeds (Pl. 26E, F) unequal; merus stout, anterior margin with long spines, thick plumose setae; external surface of carpus and propodus spinose; fingers of major chela short, stout, dark, pigmentation of propodus restricted to fixed finger; superior margin of dactyli lined with short spines, decreasing in size distally, few proximal spines on major chela, more prominent on minor chela. Ambulatory legs (Pl. 26A) stout, extensor margin with sparse long, thick, plumose and simple setae; tip of dactylus with long pigmented spine, short perpendicular subdistal spine. Male abdomen (Pl. 26D) long; somite slightly longer than broad; telson slightly longer than broad. G1 (Pl. 42C) distal 1/3 longitudinally twisted, lined with short, stout, proximally-directed subdistal setae; distal lobe longitudinally flattened, bluntly pointed.

Remarks. Forest and Guinot (1961: 91–94) gave a long account of this species, in which they mentioned that the anterolateral flange of the basal antennal segment does not fully block the orbital hiatus. This feature has a contentious history in the Chlorodiellinae (see Chapter 3). *Luniella* is diagnosed as having a flange that blocks more than half the distance of the orbital hiatus. In the other *Luniella* species, this flange completely fills the hiatus, whereas the flange in *L. scabricula* often only partially blocks the hiatus. What's more, the species exhibits variation in this feature, mostly due to age. Large specimens generally have basal antennal flanges that enter more than half the width of the orbital hiatus, sometimes completely blocking it. Beyond the incomplete lateral flange of the basal antennal segment, *L. scabricula* can be identified by its proximally twisted G1 (Pl. 42C) [versus proximally flattened and arched in other *Luniella* species (Pl. 42A, B, D)]. *Luniella scabricula* is most similar to *L. pubescens* is general shape and texture of the carapace, and anterolateral margin morphology (Pls 24B, 26B). However, the *L. scabricula* has a broader carapace with less short setae (versus narrower and covered with short setae in *L. pubescens*).

Clark & Galil (1993) reviewed *L. scabricula*'s taxonomic history, including the synonymy of *Chlorodopsis venusta* Rathbun, 1907. However, there is one other junior synonym: *Chlorodopsis natalis* Serène, 1984, a *nomen nudem* recorded in Serène (1984: 233) without a description.

Distribution. *Luniella scabricula* has a widespread IWP distribution from the Western Indian Ocean to French Polynesia. It has not been recorded from the Hawaiian Islands (Pl. 50C).

Luniella spinipes (Heller, 1861)

Pls (27, 42D, 50D)

Chlorodius niger, Ruppell 1830: 20 (part) [Red Sea]. [not *Chlorodiella nigra* (Forskål, 1775)]

Pilodius spinipes Heller 1861a: 11-12 [Red Sea]; 1861b: 340-341, pl. Ill, fig. 22 [Red Sea]. — Guinot 1964a: 12 [Red Sea; Xaafuun, Somalia]; 1964b: 68 [Abulat, Saudi Arabia]; 1967c: 268 [List]. — Derijard 1968: 1244 [Europa]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]. — Serène 1984: 243 (part), figs 143g, 148, pl. XXXIV A, B [Perim and Obock, Djibouti]. — Clark & Galil 1993: 1155, figs 15A–G, 38A,B, 39A, 44A, C [Gulf of Suez; Dahab, Sharm el Sheik, and Ghardaqa, Egypt; Sharm Yenbo, Abu Latt I., Saudi Arabia; Ras Zeili(?); Beacon I.(?), and Suakin Harbour, Sudan; Perim and Obock, and Moucha I., Djibouti; Aden, Yemen; Khasab Bay, Khor Ghubb Ali, Bukha, Mirbat, Muscat al Bustan, and Raysut, Oman; Glorioso Is.; Aldabra, African or Eagle I., Mahé, Praslin Reef, and Coetivy, Seychelles; Gan, Goidu and Male Atoll, Maldives; Salomon, Chagos Archipelago; Ile Diamant; Mayotte; Delagoa Bay, Mozambique; Nosy Be, Tamatave, Túlear, and Fort Dauphin, Madagascar; Mauritius; Andaman Is.].

Etisus spinipes Paul'son 1875: 39, pl. VI, fig. I (part) [Red Sea].

Chlorodopsis spinipes De Man 1881: 98 [Red Sea]. — Alcock 1898: 169 [Andaman Is.; Mergui Is.]. — ?Nobili 1901b: 14 [List]; 1906c: 270 [Red Sea; Djibouti; Eritrea]. — Bouvier 1915: 101 [Mauritius]. — Laurie 1915: 455 pl. XLIII, fig. 3a-d [Sudan, Red Sea]. — Balss 1924: 11 [Ras el-Millan, Tor, Senafir, Djeddah, Abu Somer?, Lidth?, Koseir, Sarso I., Berenice, Cameran?, Jambo?, Haleib?, Sharm el-Sheikh, Nawibi?, Habban, Ravaya?, Mersa Sheikh?, ?St. Johns I., Dahab]. — Monod 1938: 132

[Bay of Suez; ?Raz Zeiti, Egypt]. — Serène & Luom 1959: 321–323, 338, figs 2E, 3B, 4B, 5E, pl. IIB, IIIH [Review]. — Guinot 1958a: 178 fig. 22a, b [Mayotte].

Chlorodopsis melanodactylus, Miers 1884: 531 (part) [Etoile Island, African or Eagle I., Seychelles]. (not *Pilodius melanodactylus* A. Milne-Edwards, 1873)

Chlorodopsis woodmasoni Alcock 1898: 170 [Andaman Islands, India]; 1899, pl. 37, fig. 7. — Borradaile 1902: 261 [Male, Fadifolu, and Goifurfehendu, Lakshadweep]. — Lenz 1910: 551 [Toamasina, Madagascar]. — Rathbun 1911: 226 [Salomon, Egmont, Praslin, Coetivy, Peros, Diamont]. — Bouvier 1915: 280(103), fig. 29 [Mauritius]. — Michel 1964: 24 [Mauritius].

Chlorodopsis melanodactyla, Lenz 1905: 355 [Zanzibar, Tanzania]. (not *Pilodius melanodactylus* A. Milne-Edwards, 1873).

Chlorodopsis pugil, Klunzinger 1913: 248 (152) pl. VI(X), figs 18a-c [Review]. — Ramadan 1936: 33 (part) (Ghardaqa, Egypt, Red Sea). [not *Luniella pugil* (Dana 1852)]

Chlorodopsis pilumnoides, Barnard 1955: 3 (part) [List]. — Guinot 1967: 268 (part) [List]. [not *P. pilumnoides* (White, 1848)]

Chlorodopsis pubescens, Serène 1977: 51 [List]. [not *Luniella pubescens* (Dana, 1852)].

Pilodius aff. *spinipes* Serène 1984: 244, fig. 143h, pl. XXXIV C [Nosy Be, Tolear, Fort-Dauphin, Madagascar; Ile Maurice; Ile Glorieuses; Mayotte, Iles Comoros; Ile Aldabra].

Material examined. *Red Sea:* 2 males, 14.6 × 9.2 – 9.3 × 5.7, 3 females, 6.8 × 4.3 – 12.9 × 8.1, 1 ovigerous female (damaged) (UF 32990*), BDJRS-0795, DJRS-039, 2–20 m, 22.2741° 39.0512°, seaward reef slope and front of, Thuwal, Saudi Arabia, coll. M. Berumen & G. Paulay, 10 October

2012. — 1 male, 9.8 × 6.3, 1 female, 9.1 × 5.6 (UF 32959*), BDJRS-0677, DJRS-033, 4–7 m, 22.4301° 38.9952°, lagoon of shelf reef, Shark Reef, Thuwal, Saudi Arabia, coll. G. Paulay, 7 October 2012. — 1 male, 12.9 × 8.2 (UF 32826), BDJRS-0190, DJRS-007, 8–13 m, 11.976° 43.365°, in dead coral, reef slope, E of Obock, NE Gulf of Tadjoura, Djibouti, coll. G. Paulay, 29 September 2012. — 1 male, 17.4 × 11.5 (UF 32823), BDJRS-0185, DJRS-007, 8–13 m, 11.976° 43.365°, reef slope, under dead coral, E of Obock, NE Gulf of Tadjoura, Djibouti, coll. G. Paulay, 29 September 2012.

Persian Gulf: 1 male, 7.5 × 4.8, 3 females, 4.6 × 3.0 – 7.9 × 5.0, 1 ovigerous female, 7.9 × 5.2 (USNM 106019), 0–4 m, shallow reef, near station 7, Jaraid Island, Persian Gulf, Arabian Sea, coll. C. Dawson, 4 October 1956. — 1 male, 7.7 × 5.0 – 10.8 × 6.7 (USNM 93954), Sta. HO-7, Persian Gulf, Arabian Sea, coll. Hydrographic office.

Gulf of Oman: 1 male, 8.5 × 5.4 (UF 7802*), BOMAN-478, GP-Loc-820, 4–15 m, 23.5271° 58.7395°, reef slope in outer part of embayment, SE of Muscat, Bandar Karyan, Gulf of Oman, Oman, coll. V. Bonito *et al.*, 28 January 2005. — 1 female, 11.8 × 7.6 (UF 18026*), BOMAN-391, GP-Loc-819, 0–1 m, intertidal rocky shore w/karst, near Muscat, Qurm Beach, Oman, coll. V. Bonito *et al*. — 2 males, 6.7 × 4.5 – 7.7 × 5.2 (UF 7644), BOMAN-052, GP-Loc-800, 0–16 m, 23.6817° 58.4971°, under? Coral, reef slope off island, near Muscat, W side of Fahl Island, Oman, coll. V. Bonito, *et al.*, 16 January 2005.

Mayotte: 1 female, 11.7 × 7.7 (UF 13571*), MAY08-011, MAYO8-St1, 1–2 m, -12.9474° 45.0998°, cryptofauna, reef flat, Mbouanasta, Mayotte Island, Comoros Islands, coll. A. Anker & F. Michonneau, 29 May 2008. — 1 female, 13.4 × 8.6 (UF 13619*), MAY08-188, MAY08-St5, 3–4 m, -12.8593° 45.2686°, cryptofauna, reef flat, Passe en S, Mayotte, Comoros Islands, coll. A. Anker & F. Michonneau, 2 June 2008.

Madagascar: 1 ovigerous female, 14.0 × 9.0 (UF 14327*), NBE-1422, MGNW-23, 1–3 m, -13.4139° 48.3056°, seagrass flat and adjacent sand/reef slope, off Lokobe Reserve, across bay from CNRO complex, Nosy Be, coll. A. Anker *et al.*, 16 May 2008. — 1 male, 14.7 × 9.7 (UF 14359*), NBE-1505, MGNW-23, 1–6 m, -13.4139° 48.3056°, seagrass flat and adjacent sand/reef slope, rubble, off Lokobe Reserve, across bay from CNRO complex, Nosy Be, coll. G. Bakary *et al*., 16 May 2008. — 1 female, 11.1 × 8.0 (UF 14029*), BMADA-0424, MGNW-48, 2–12 m, -13.5802° 47.8201°, basalt shore, pavement, wall, off N side, Nosy Iranja, Madagascar, coll. G. Bakary *et al.*, 24 May 2008. — 1 male, 15.3 × 10.1 (UF 14361*), NBE-1508, MGNW-23, 1–6 m, -13.4139° 48.3056°, rubble, seagrass flat and adjacent sand/reef slope, off Lokobe Reserve, across bay from CNRO complex, Nosy Be, Madagascar, coll. G. Bakary *et al*., 16 May 2008.

Chagos: 1 female, 13.60 × 8.65 (ZRC 2013.0769*) CH0459, 10m approx., dead branching coral heads, lagoon, Peros Banhos Chagos Archipelago, coll. C. Head & H. Koldeway, 23 February 2013. — 1 male, 9.10 × 5.80 (ZRC 2013.0768*), CH0440, 10m approx., dead branching coral heads, lagoon, Peros Banhos Chagos Archipelago, coll. C. Head & H. Koldeway, 23 February 2013.

Maldives: 3 males, 11.1 × 7.6 – 17.8 × 11.5, 2 females, 14.2 × 9.4 – 14.8 × 9.5 (ZRC 2007.0740), Laamu Atoll, Maldives, coll. A. Kumar, November 2007.

Diagnosis. Carapace (Pl. 27B) transversely hexagonal, ca. 1.6 broad as long; surface granulate, sometimes covered in short, light-colored setae; regions well defined; 2M, 3M entire. Frontal (Pl. 27C) submedian lobes convex, separated by wide, shallow U-shape notch, margin lined with short spines; lateral lobes triangular. Anterolateral margin with 4 teeth; tooth 1 small; teeth 2–3 larger, with anteriorly directed apical spines; tooth 2 often with posterior ancillary spine. Anterolateral angle of basal antennal segment expanded, completely blocking orbital hiatus. Pterygostomial region minutely granulate, bearing thick, plumose setae. Chelipeds (Pl. 27E, F) unequal; merus stout, anterior margin with long spines, thick plumose setae; external surface of carpus and propodus often covered with short setae, spinose, spines short, stout; fingers of major chela short, stout, dark, pigmentation of propodus restricted to fixed finger; superior margin of dactyli lined with short, stout spines, decreasing in size distally, more prominent on minor chela. Ambulatory legs (Pl. 27A) stout, setose, setae simple or thick plumose; tip of dactylus with long pigmented spine, short perpendicular subdistal spine. Male abdomen somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 42D) distal 1/3 curving ventrally, with stout, proximally-directed, dorsal subdistal setae; long, stout ventral subdistal setae; distal lobe relatively narrow, laterally flattened, arched, curving ventrally, ultimately rounded.

Remarks. The substantial morphological variation of *Luniella spinipes* was documented by Serène & Luom (1959), Guinot (1964), Serène (1984), and Clark & Galil (1993). The carapace of some specimens is close to *L. scabricula* in having shallowly defined regions, shorter anterolateral teeth, less spinose chelipeds, and a sparsely setose carapace. In other specimens, *L. spinipes* is more similar to *L. pugil* in having deeply defined regions of the carapace with few or no setae, heavily spinose chelipeds, and a similar spinose anterolateral margin with teeth that are long and without ancillary granules or spines. The species is difficult to identify due to these variations. Clark & Galil's (1993) key to the species of *Pilodius* indicates that *L. spinipes* possesses carapace regions 2M that are longitudinally divided (as in UF 14029) and lateral regions lacking cornute, conical tubercles. However, some specimens have entire 2M regions and lateral, conical granules (e.g., UF

14361). Furthermore, Clark & Galil's (1996: 1155) diagnosis of *L. spinipes* states that 2M is *partially* divided, in conflict with their key.

Serène & Luom (1959) sank *Chlorodopsis woodmasoni* Alcock, 1898, as it falls within the variation of *L. spinipes.* Sakai (1999) placed *Cancer eurynome* Herbst, 1801 in *Pilodius*. In Sakai's work, Türkay commented that the species looks similar to *L. spinipes*. However, the East Indies locality of the specimen is extralimital to *L. spinipes*, and the specimen appears to be *P. pilumnoides.*

Given the variation in external morphology of *P. spinipes*, examination of the G1 is important for identification. *Luniella spinipes*, *L. pubescens*, and *L. pugil* have G1s with longitudinally flatten, arched apical lobes (Pl. 42A, B, D) [versus distally twisted in *L. scabricula* (Pl. 42C)]. *Luniella spinipes* and *L. pugil* differ from *L. pubescens* in having relatively stout subdistal setae (versus long and thin in *L. pubescens*). The G1s of *L. spinipes* and *L. pugil* are very similar. However, *L. spinipes* has a G1 with stout, relatively long, more numerous subdistal setae on the ventral side (versus spinose with few or no long setae in the ventral, subdistal area).

Distribution. *Luniella spinipes* is restricted to Red Sea, Persian Gulf and Indian Ocean (Pl. 50D).

Pilodius Dana, 1851

Key to the Species of *Pilodius*.

1. Dorsal surface of carapace covered with tomentum............................2
– Dorsal surface of carapace covered with short, stout, simple setae.....4

2. Carapace regions covered with large pearliform granules unobscured by setae. Extensor margin of ambulatory legs fringed with row of thick, plumose setae...*P. areolatus*

– Carapace regions granulate; granules relatively small, laterally conical, often obscured by setae. Extensor margin of ambulatory legs with relatively sparse setae not forming fringe.....................................3

3. Pigmentation of male chelae completely encircling propodus (Pl. 31E, F). G1 apex ovate (Pl. 43D)...*P. miersi*

– Pigmentation of male chelae restricted to inferior half of propodus (Pl. 29E, F). G1 with elongated bent or recurved apical lobe (Pl. 43B)..*P. granulatus*

4. Carpus and propodus of ambulatory legs with longitudinal, setae-fringed grooves...*P. moranti*

– Carpus and propodus of ambulatory legs without longitudinal, setae-fringed grooves..5

5. Male thoracic sternum glabrous or with few scatter posterior setae. G1 apex hooked (Pl. 44B)...*P. nigrocrinitus*

– Male thoracic sternum with numerous simple, dark, short setae (sometimes worn). G1 apical lobe curved but not hooked..................6

6. G1 apical lobe relatively narrow (Pl. 44C).......................*P. pilumnoides*

– G1 apical lobe relatively broad (Pl. 43C)..............................*P. maotieni*

Pilodius areolatus (H. Milne Edwards, 1834)

Pls (28, 43A, 51A)

Chlorodius areolatus H. Milne Edwards 1834: 400 [type locality = Australia]. — White 1847: 18 [Philippines]. — Adams and White 1849: 41 [Philippines]. — Hess 1865: 135 [Australia].

Chlorodius perlatus MacLeay 1838: 59 [South Africa]. — Krauss 1843: 31 [South Africa].

Xantho dehaanii Krauss 1843: 29, pl. I, fig. 2 [South Africa].

Actaeodes affinis Dana 1852a: 78 [Tahiti]; 1853: 197; 1855: pl. XI, fig. 3 [Atlas]. — Stimpson 1907: 43 [Ryukyu Is., Japan].

Etisodes caelatus Dana 1852a: 77 [Wake Island]; 1853: 188; 1855, pl. 9, fig. 4 [Atlas]. — Whitelegge 1897: 131.

Actaea affinis A. Milne-Edwards 1865: 263 [Review]. — Haswell 1882: 45 [Port Jackson, Australia]. — Whitelegge 1889: 226 [List]. — Borradaile 1900: 583 [Rotuma]; 1902: 254 [Male; Goifurfehendu; Fadifolu; Minikoi]. — Grant and McCulloch 1906: 11 [Mast Head I., Australia]. — Rathbun 1906: 852 [Hawaiian Is.]. — Stimpson 1907: 43 [Ryukyu Is., Japan]. — Rathbun 1907: 42 [Makemo]; 1911: 219 [Peros, Coin; Salomon; Egmont reef; Coetivy]; 1914: 658 [Hermite]. — Balss 1922: 121 [List]. — Edmonson 1923: 15 [Palmyra; Fanning I.].

Chlorodopsis areolatus A. Milne-Edwards 1873: 231, pl. VIII, fig. 8 [New Caledonia]. — Hilgendorf 1879: 790 [Ibo, Mozambique]. — Richters 1880: 140, 148 [Iles Fouquets]. — Haswell 1882: 54 [Port Jackson, Australia]. — Miers 1884: 217, 532 [N Australia; Darros I., Seychelles; Mozambique]. — Muller 1887: 474 [Trincomoli, Sri Lanka]. — Whitelegge 1889: 227 [List]. — Ortmann 1893: 470 [Samoan Is.; Amami Oshima, Japan]. — Alcock & Anderson, 1894: 200 [Palk Strait]. — Bouvier 1915: 278, figs 30, 31 [Mauritius]. — Balss 1922: 131 [Okinawa, Japan]. — Ward 1932: 251 [Capricorn Group, Australia]. — Michel 1964: 24 [Mauritius].

Actaeodes tomentosus Miers 1886: 135 [Samboangan, Philippines]. — Lanchester 1900: 734 [Singapore].

Chlorodopsis areolata De Man 1890: 54 [Fiji Is.]. — Alcock 1898: 166 [Andaman Islands, Nicobar Islands, India; Sri Lanka]. — Lenz 1905: 354, pl. 47, fig. 8 [Zanzibar, Tanzania; Aldabra]; 1910: 551 [Europa Island, Toliara, and Antongil Bay, Madagascar]. — Laurie 1906: 405 [Galle, Sri Lanka]. — Nobili 1906c: 269 [Red Sea]. — Rathbun 1906: 858 [Hawaiian Islands]. — Nobili 1907: 396, pl. 2, fig. 3 [Mangareva, Hikueru, and Marutea Sud, Tuamotu Archipelago]. — Calman 1909: 705 [Christmas Island]. — Stebbing 1910: 300 [List]. — Klunzinger 1913: 250 [Red Sea]. — Sendler 1923: 38. — Odhner 1925: 36 [Review]. — Hale 1929: 70 [Dirk Hartog I., Australia]. — Montgomery 1931: 443 [Wooded I. and Long I., Abrolhos]. — Edmondson 1933: 250, fig. 152b [Review]; 1962: 269, fig. 19a [Hawaii]. — Balss 1935: 139 [Shark Bay, Australia] ; 1938a: 62 [Nauru; Aranuka, Apamama, Tamana, Nukunya, Beru and Taritari, Gilbert Islands; Viti Levu and Namuka, Fiji Island; Nukufetau, Ellice Islands; Ailinglablab, Marshall Islands]. — Miyake 1939: 215, 237. — Sakai 1939: 502, pl. 97, fig. 3 [Loo Choo, Japan]; 1956: 40. — Tweedie 1947: 27 [List]; 1950b: 121 [Cocos (Keeling) Islands]. — Barnard 1950: 214, figs 39d, e [Durban and Port St. Johns, South Africa]. — Holthuis 1953: 15 [Onotoa, Gilbert Islands; Homohomo Island, Tuamotu Islands]. — Guinot 1958a: 176, figs 21a, b [Mayotte]. — Serène and Luom 1958: 96, fig. 2, pls IA, Via [Vietnam]; 1959, fig. 5a [Review]. — Sankarankutty 1962: 138, figs 24, 25 [Neil Island, India]. — Garth 1964: 140 [Enewetak]. — Ooishi 1964: 199. — Kensley 1970: 104 [Inhambane, Mozambique].

Phymodius ungulatus, Boone 1934: 143 [List]. — Serène and Luom 1958: 96 [List]. — Serène 1984: 241 [List]. [not *Cyclodius ungulatus* **(**H. Milne Edwards, 1834)]

Pilodius areolatus Forest and Guinot 1961: 90 [Hikeuru; Tahiti]. — Guinot 1962b: 237 [Lhaviyani Atoll, Maldives]; 1964b: 66 [Aldabra]; 1967: 267 [List]. — Sankarankutty 1966: 48, 50 [Seychelles; Mauritius]. — Derijard 1968: 1244 [Europa Island]. — Serène 1968: 80 [List]. — Ooishi 1970: 93 [Ogasawara]; Sakai 1976: 460, pl. 164, fig. 1 [Yoron I. and Ishigaki I., Japan]. — Takeda and Miyake 1976: 110 [Ogasawara Is., Japan]. — Serène *et al*. 1976: 18 [Ambon I., Indonesia]. — Takeda and Nunomura 1976: 62, 72 [?????]. — Peyrot-Clausade 1977a: 27 [Tulear, Madagascar]. — Serène 1977a: 51 [Seychelles]. — Chen & Lan 1978: 267, fig. 8:2, pl. 8, fig. 30. [Xisha Islands]. — Takeda 1978: 40 [Kyushu, Japan]. — Serène 1984: 241, figs 143c, 144, pl. 33C [Fort Dauphin, Madagascar; Iles Glorieuses; Mayotte, Iles Comoros; Ile Remise(?) and Aldabra, Iles Seychelles; Reunion Island]. — Dai *et al.* 1986: 305, pl. 43(2), fig. 165B(1) [Review]. — Titgen 1987: 108 [Hawaii]. — Takeda 1989: 165, 178 [Kakeroma-jima, Japan]. — Dai & Yang 1991: 328, pl. 43(2), fig. 165B(1) [Review]. — Clark & Galil 1993: 1125, figs 1, 17, 31(A), 40(A) [near Watamu, Kenya; Reunion I.; Coetivy, Seychelles; Coin, Chagos Is.; Fadiffolu Atoll, Minijol Atoll(?), Goifurfehendu Atoll, and Hulule, Maldives; Weligama, Sri Lanka; Cocos Keeling Is.; Christmas I.; Okinawa, Japan; Philippines; Masthead, Port Jackson, Heron I., Lady Elliot I., South I., Wreck Reef, and Middleton Reef, Australia; Palau I.; Platier du Phare Amedee, New Caledonia; Moorea I.; Bora Bora, Society Is.; Oahu, Hawaiian Is.; Viti Levu I and Rotuma I., Fiji].]. — DeFelice *et al*. 1998: 16 [Midway Atoll, Hawaiian Is.]. — Coles *et al.* 2001: 54 [List]. — DeFelice *et al.* 2002: 30, 72 [French Frigate Shoals, Hawaiian Is.]. —

Coles *et al*. 2002a: 271, 334 [Oahu, Hawaii]; 2002b: 140, 194 [Oahu, Hawaii]. — Davie 2002: 522 [List]. — Coles *et al*. 2004: 65 [Kauai, Hawaiian I.]. — Godwin & Bolick 2006: 39, 49 [Honolulu, Hawaiian Is.]. — Hoover 2006: 282, color photograph [Hawaiian Is.]. — Coles *et al.* 2008: 63 [List]. — Ng *et al*. 2008: 197 [List]. — Coles & Swenson 2010: 87 [List]. — Felder & Thoma 2010: 136 [Hawaii].

Pilodius areolata Amerson & Shelton 1976: 76. — Kensley 1981: 45 [List].

Actaea perlata Ward 1942: 88 [Salomon Islands, Chagos Archipelago].

Chlorodopsis areolata var. *brandonensis* Ward 1942: 97, pl. 6, fig. 3 [St. Brandon, Mauritius].

Material examined. *Comoros Islands:* 1 female, 16.1 × 11.3 (UF 20185), Stn. MAY08-St0, Mayotte Island, Comoros Islands, France, coll. A. Anker & F. Michonneau, May 2008. — 1 male, 13.2 × 9.3 (UF 13553), Stn. MAY08-St2, -12.760527° 45.067972°, 2–3 m, under rocks, reef flat and fringing reef, Tanaraki, Mayotte Island, Comoros Islands, France, coll. A. Anker & F. Michonneau, 30 May 2008.

Scattered Islands: 1 male, 13.3 × 10.3 (UF 20586), Stn. JDNO-1, -17.07825° 42.7306°, 0–1 m, reef flat, Iles Eparses, Juan de Nova, S coast, Juan de Nova Island, Scattered Islands, France, coll. H. Bruggemann & M. Malay, 26 April 2009.

Madagascar: 1 male, 10.5 × 7.6 (UF 14128), Stn. MGNW-48, -13.58018° 47.82011°, 2–12 m, basalt shore, wall, pavement, exposed reef slope, Nosy Iranja, off N side, Madagascar, coll. G. Bakary *et al.*, 24 May 2008. — 1 male, 11.6 × 8.6 (UF 14206*), Stn. MGNW-18, -13.4892° 47.9767°, 0–2 m, Nosy Ankazoberavina, S peninsula, near Nosy Be, Madagascar, coll. G. Paulay, 13 May 2008.

Reunion Island: 1 male, 16.75 × 11.45 (UF 12807*), BREU-1194, SWIO-2, 0–2 m, -21.1072° 55.2489°, Varangue du lagon, Reunion Island, Mascarene Islands, coll. H. Bruggemann *et al.*, 6 August 2007. — 1 male, 17.8 × 12.0 (UF 12579*), Stn. SWIO-FM33, -21.0787° 55.2256°, 0–2 m, Saint-Gilles, Chez Go, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 25 July 2007. — 1 male, 12.4 × 8.8 (UF 12585*), Stn. SWIO-FM34, -21.1769° 55.2873°, 0–2 m, Saint-Leu, Snack 46, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 26 July 2007. — 1 female, 13.1 × 9.1 (UF 12582*), Stn. SWIO-FM33, -21.0787° 55.2256°, 0–2 m, Saint-Gilles, Chez Go, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 25 July 2007. — 1 male, 14.2 × 10.2 (UF 12584*), Stn. SWIO-FM34, -21.1769° 55.2873°, 0–2 m, Saint-Leu, Snack 46, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 26 July 2007. — 1 female, 12.4 × 8.6 (UF 12607*), Stn. SWIO-FM39, -21.0805° 55.2238°, 0–2 m, La Saline, Toboggan, Reunion Island, Mascarene Islands, France, coll. N. Hubert & F. Michonneau, 2 August 2007.

Seychelles: 2 males, 19.66 × 13.54 – 20.57 × 14.13 (USNM 41211), Coetivy, Western Indian Ocean, coll. H. M. S. Sealark, J. Stanley Gardiner, 1905.

Mauritius: 1 male, 11.1 × 7.8, 1 female, 12.6 × 8.7 (USNM 81440), Mauritius, coll. N. Pike.

Chagos: 4 males, 9.13 × 6.69 – 18.27 × 12.02, 2 females, 15.23 × 10.70 – 16.03 × 11.18 (USNM 41212), Egmont Reef, Western Indian Ocean, coll. H. M. S. Searlark, Acc. No. 51720, 1905.

Maldives: 5 males, 11.9 × 8.6 – 21.2 × 14.4, 1 female, 15.3 × 10.6 (ZRC 2007.0738), Laamu Atoll, Maldives, coll. A. Kumar, November 2007.

Cocos-Keeling Islands: 24 males (largest = 20.70 × 14.35) 18 females (NMS.1965.11.11.28–37), Cocos Keeling Island, Indian Ocean, coll. C. Gibson-Hill, 1941.

Indonesia: 1 male, 14.0 × 10.6 (ZRC 2013.1627*), Stn. BL11-012, BALI-0382, 1–2 m, snorkel, hand, under rock, coral reef, sea grass, sand, near jetty, Sombu, Wanci, Sulawesi, Indonesia, coll. 24 June 2011.

Taiwan: 1 female, 12.0 × 8.1 (USNM 1181264), Liuqui Shiang, Pintung County, Taiwan, coll. J. Huang, 18 March 2006.

Australia: 1 male (damaged) (NMS.1965.11.11.27), Long Reef, bollary nr. Sydney, coll. M. Ward. — 1 male, 19.45 × 13.10 (ZRC 2013.0726) NING 0072, 0.5–2 m, -22.6234, 113.6436 rubble extraction, dead coral ledge on sand, overgrown with algae, with *Tridacna*, Ningaloo Reef, near Point Cloats, Western Australia, coll. R. Lasley, 16 May 2010. — 1 male, 11.0 × 7.8 (USNM 98812), coral reef, Myora, Moreton Bay, Stradbroke Island, Queensland, Australia, coll. S. Kellner. — 1 female, 21.7 × 14.7 (USNM 1181324), intertidal, Capricorn Group Islands, Queensland, Australia, coll. S. Rosso, 20 July 1955. — 1 male, 22.3 × 16.5 (UF 21977*), Stn. NIN09-St-47, -22.55114° 113.6632°, 1–2 m, in rock, lagoon, Ningaloo Reef, South Lefroy Bay, Western Australia, Australia, coll. R. Lasley, May 2009. — 1 male, 19.3 × 13.3 (UF 21480*), Stn. NIN09-St-7, -22.74152° 113.6836°, 2–3 m, under rock, back reef, patchy corals on sand, Ningaloo Reef, S shallow bommies, Western Australia, Australia, coll. R. Lasley, 15 May 2009. — 1 female, 20.4 × 14.0 (UF 21401*), Stn. NIN09-St-1, -22.67552° 113.68403°, 0–1 m, under rock, lagoon, sand bottom with *Sargassum* patches, Ningaloo Reef, in front of Ningaloo Station, Western Australia, Australia, coll. F. Michonneau, 14 May 2009. — 1 ovigerous female, 18.1 × 12.4 (UF 25557*), Stn. HI09-093, -23.4321° 152.04457°, 18–19 m, reef crest, Heron Island, Sykes Reef, Queensland, Australia, coll. 23 November 2009. — 1 female, 18.8 × 13.0 (UF

24973*), Stn. HI09-023, -23.2708° 151.9336°, 1–2 m, in rubble, reef crest, Heron Island, Broomfield Reef, Queensland, Australia, coll. R. Lasley, 15 November 2009. — 1 male, 16.1 × 11.0 (UF 24893*), Stn. HI09-019, -23.43135° 152.03375°, 1–2 m, under rock, reef crest, reef flat, Heron Island, Sykes Reef, Queensland, Australia, coll. F. Michonneau & R. Lasley, 14 November 2009.

Japan: 1 male, 7.1 × 5.1 (ZRC 1992.4994), Kunri-Hama Beach, Sesoka Island, Okinawa, Japan, coll. P. Ng & D. Chia, April 1992. — 1 male, 13.0 × 9.0 (UF 26943*), Stn. GUOK10-St-067, 24.421202° 123.802599°, 0–1 m, mostly under rocks, reef at low tide, Iriomote, Uehara, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans & F. Michonneau, 10 July 2010. — 1 female, 9.0 × 6.5 (UF 28639*), Stn. FMOK11-St-19, 26.444199° 127.772746°, 0–1 m, under rock, exposed fore reef, Maeda, Okinawa, Ryukyus, Japan, coll. F. Michonneau & Y. Ryuta, 14 May 2011.

Papua New Guinea: 1 female, 8.6 × 6.2 (USNM 134586), Bougainville Island, Papua New Guinea, coll. W. Bartos.

Mariana Islands: 1 male, 11.7 × 8.0, 2 females, 9.3 × 6.4 – 10.7 × 7.7 (USNM 1184662), 8 m, in front of marine lab, reef front, Pago Bay, Guam, coll. R. Kropp, 9 November 1984. — 1 male, 5.0 × 3.6, 1 female, 9.9 × 6.8, 1 ovigerous female, 10.0 × 6.8 (USNM 1181212), 13 21 36 N 144 38 42 E, intertidal low tide, Nimitz Beach Drive and boat launch area, 1 km ENE of Anae Island, Guam, coll. R. Bolland, 20 August 1983. — 1 male, 9.8 × 7.0 (USNM 1184651), 12 m, Pagua Patch Reef, Double Reef, Guam, coll. R. Kropp & J. Dominguez, 24 August 1984. — 4 males, 8.0 × 5.9 – 16.8 × 11.2, 3 females, 6.3 × 4.5 – 15.4 × 10.5, 3 ovigerous females, 9.3 × 6.4 – 12.6 × 8.7 (USNM 1181326), in coral, Saipan Island, Northern Mariana Islands, coll. A. Banner, 1945. — 1 male, 13.7 × 9.5 (UF 2840), Stn. ZZZ-087523, 13.5° 144.8°, 1–4 m, under and among rocks, Asan Point, Guam Island, Mariana

Islands, USA, coll. H. Conley, 3 July 2002. — 1 male, 9.6 × 6.7 (UF 4151), Stn. BGUAM-100, 13.5° 144.8°, 0 m, intertidal under rocks, outer reef flat, Hagatna Bay, E Side, Guam Island, Mariana Islands, USA, coll. G. Paulay, 2003. — 1 male, 4.4 × 3.3 (UF 13372), Stn. FM-St-GU08-08, 13.426695° 144.796052°, 0–1 m, under rocks, fore reef, Mangilao, Pago Bay, Guam Island, Mariana Islands, USA, coll. F. Michonneau & S. Kim, 17 March 2008.

Caroline Islands: 1 male, 11.1 × 7.8 (USNM 1181366), intertidal, S reef flat, Okat, Kosrae Island, Caroline Islands, Micronesia, coll. L. Eldredge, 27 May 1979. — 1 male, 11.7 × 8.3 (USNM 106611), inner reef flat, reef N of NW end of island, Falarik Island, Ifalik Atoll, Yap Islands, Caroline Islands, Yap, Micronesia, coll. D. Abbott, 2 October 1953. — 1 ovigerous female, 14.4 × 10.0 (UF 3894*), Stn. BPAL-101, 7.19333° 134.4518333°, 0–3 m, reef top and back reef, Ngchesau Reef, Palau, coll. G. Paulay, 7 March 2003. — 2 males, 15.0 × 10.5 – 16.1 × 11.4, 1 ovigerous female, 13.7 × 9.6 (UF 5271*), Stn. JAS-PON-063, 6.758° 157.995°, 0–1 m, rock, reef flat, Ant Atoll Channel, Entry Channel to Inner Lagoon, Ant Atoll, Caroline Islands, Federated States of Micronesia, coll. J. Starmer, 12 March 2003.

Solomon Islands: 1 male, 13.5 × 9.6 (USNM 1181337), Solomon Islands, coll. United States Navy. — 2 males, 9.8 × 6.9 – 10.6 × 7.3, 1 damaged male, 1 female, 11.4 × 7.8 (USNM 1181312), Green Island, Solomon Islands, coll. W. Bartos. — 1 female, 14.9 × 10.1 (UF 2551), Stn. ZZZ-087065, 3–20 m, among rocks and coral, Near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 13 February 2002. — 1 female, 9.7 × 6.9 (UF 3395*), Stn. ZZZ-087900, 3–5 m, among dead coral and rocks, near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 10 February 2002. — 1 male, 6.5 × 5.2 (UF 2518*), Stn. ZZZ-087064, 3–5 m, among rocks and coral, near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 14 February 2002.

Vanuatu: 1 male, 22.45 × 15.00, (ZRC 2013.0724), Stn. VM46, 15°34.5'S, 167°12.3'E, freshwater (?), Aoré Island, Vanuatu, coll. 3 October 2006. — 3 males (largest = 16.05 × 11.20), 3 females (ZRC 2013.0725), Stn. LM19, intertidal, 15°38.5'S, 167°15.1'E, E Malo Island, Vanuatu, 5 October 2006. — 1 male, 17.5 × 12.1, 1 female, 12.3 × 9.5 (ZRC 2013.1628), Stn. AT52, 52-62 m, 15°31.5'S, 167°12.7'E, Segond Channel, Vanuatu, coll. Santo Marine Biodiversity Survey, 2 October 2006. — 1 male, 15.1 × 10.6 (ZRC 2013.1629), Stn. VM16, 15°37.7'S, 167°11.0'E, intertidal, sand and coral, Bruat Channel, N coast of Malo Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 18 September 2006. — 1 ovigerous female, 16.9 × 12.6 (UF 8567*), Stn. ZZZ-093421, -15.333° 166.75°, Bokissa Island, Sanma Province, Vanuatu, coll. C. Meyer, 23 January 2005.

Marshall Islands: 1 male, 18.4 × 12.0 (USNM 102941), Romuk Island (Romurikku), Bikini Atoll, Ralik Chain, Marshall Islands, coll. L. Schultz, 13 May 1946. — 1 female, 8.0 × 5.7 (USNM 266912), ocean side, Igurin Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. D. Reish, 27 August 1956. — 3 males, 8.9 × 6.3 – 16.2 × 11.2 (USNM 1181292), Arno Atoll, Ratak Chain, Marshall Islands, coll. R. Hiatt. — 1 male, 7.8 × 5.6 (USNM 1181331), Kabbenbock Island, Jaluit Atoll, Ralik Chain, Marshall Islands, coll. H. Rehder, 20 October 1960. — 1 male, 13.8 × 9.4 (USNM 1181342), lagoon reef, Latoback Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. F. Bayer & F. Zimmerman, 18 August 1947. — 1 male, 13.1 × 9.2 (UF 13758), Stn. FM-St-MAJ08-02, 7.16517° 171.03608°, 0–2 m, under rocks, reef flat, sand, sea grass bed, corals, rubble, Laura, ocean side, N end of the island, Majuro Atoll, Marshall Islands, Republic of the Marshall Islands, coll. F. Michonneau & S. Kim, 4 April 2008. — 3 males, 9.0 × 6.4 – 16.0 × 10.8, 1 female, 11.2 × 7.8 (UF 13416*), Stn. FM-St-MAJ08-08, 7.12419° 171.35625°, 0 m, under rocks, intertidal rocks and sea grass, Rita, channel (N end of main island), Majuro Atoll, Marshall Islands, Republic of the Marshall Islands, coll. F. Michonneau & S. Kim, 7 May 2008.

Fiji: 2 females, 13.1 × 9.0 – 14.8 × 10.1 (USNM 1181355), Maku Suva Reef, Fiji, coll. 8 June 1922. — 1 female, 12.9 × 8.9 (USNM 1181363), Makusuva Reef, Viti Levu Island, Fiji, coll. State University of Iowa, 9 June 1922.

Samoan Islands: 5 males, 12.5 × 8.7 – 19.4 × 13.1, 3 females, 10.3 × 7.0 – 11.4 × 7.8 (USNM 1181369), Pago Pago, Tutuila Island, American Samoa, coll. United States Fish Commission, August 1902. — 4 males, 14.9 × 10.2 – 19.8 × 14.2 (USNM 1181329), coral reef, Apia, Upolu Island, Western Samoa, coll. United States Fish Commission, July 1902. — 1 female, 10.8 × 7.6 (USNM 1181349), Pago Pago, Tutuila Island, American Samoa, coll. United States Fish Commission, August 1902.

Niue: 1 male, 8.1 × 6.1 (UF 2241), Stn. BNIUE-345, -19.1° -169.9°, 0–5 m, in rubble under rocks, reef flat, pools, Namukulu, Limu Reef Flat, Niue Island, Niue Island, Niue Island, coll. B. Holthuis & G. Paulay, 7 October 1991.

Cook Islands: 1 female, 5.6 × 4.2 (UF 11716*), Stn. MRARO-001, -21.2333° -159.7667°, 0–5 m, reef flat, Vaima'anga (S Coast) near Captain Cook Resort, in front of Teina's brother's house, Rarotonga Island, Cook Islands, Cook Islands, coll. M. Malay, 23 June 2006. — 1 male, 16.3 × 11.4 (UF 10334*), Stn. MRARO-002, -21.25667 -159.8168333, 0–5 m, , lagoonar pool in reef flat, Kavera (W Coast), near Rarotongan Beach Resort, Rarotonga Island, Cook Islands, Cook Islands, coll. M. Malay, 18 June 2006.

Johnston Atoll: 1 male, 17.7 × 12.3, 1 ovigerous female, 17.7 × 12.6 (USNM 81466), Johnston Island, Johnston Atoll, United States Minor Outlying Islands, coll. C. Edmondson, 1923.

Kiribati: 1 male, 17.9 × 12.5 (USNM 81439), Gilbert Islands, Kiribati, coll. A. Garrett. — 1 female, 13.3 × 9.2 (USNM 94194), Onotoa Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 8 August 1951. — 1 female, 18.0 × 12.3 (USNM 1181318), 0 m, gear: poison, reef, Kanton Island, Kanton Island, Kiribati, coll. L. Schultz, 13 May 1939. — 4 males, 16.5 × 11.5 – 18.3 × 12.4, 1 female, 14.5 × 10.0 (USNM 1181315), 2–3 m, Canton Island, Phoenix Island, Kiribati, coll. C. Ely, 1941. — 1 female, 16.7 × 11.7 (USNM 93975), 1 m, Onotao Atoll, Gilbert Islands, Kiribati, coll. A. Banner, 1 August 1951. — 1 female, 6.9 × 5.0 (UF 14928), Stn. KIR-A, 2.0083° -157.3961°, 0–1 m, reef flat & crest, around Captain Cook Hotel, N part of island, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay, 21 August 2005. — 1 male, 16.2 × 11.0 (UF 10592*), Stn. GP-Loc-823, 2.0087° -157.4893°, 0–2 m, under rocks, reef flat & reef front, just N of wharf, off Anchorage, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay, 3 2005. — 1 female, 13.7 × 9.3 (UF 10723*), Stn. KIR-A, 2.0083° -157.3961°, 0–1 m, near shore land, shore, and reef flat, around Captain Cook Hotel, N part of island, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay, 21 August 2005.

Hawaiian Islands: 1 male, 19.35 × 13.50 (UF 12176*), BFFS-647, FFS-0106, 15 ft, 23.873° -166.2337°, hand collected, back reef, under rocks, French Frigate Shoals, Hawaiian Islands, coll. C. Pitman *et al.*, 18 October 2006. — 2 ovigerous females (largest = 12.75 × 9.00) (ZRC 2000.0437), intertidal area, Malpalaoa Beach, near Maili Point, Maili, Waianae Coast, leeward side of Oahu, Hawaii, coll. P. Ng & S. Tan, 22 January 2000. — 1 male, 12.8 × 8.9, 1 ovigerous female, 11.2 × 7.7 (USNM 99147), Waikiki Reef, Oahu Island, Hawaii, United States, coll. C. Cutress, 18 February 1950. — 2 males, 16.1 × 11.2 – 18.7 × 12.9, 4 ovigerous females, 12.9 × 9.0 – 14.4 × 10.0 (USNM 29381), 25 46 N 171 44 W, Laysan Island, Hawaii, United States, coll. Hawaiian Explorations, Albatross R/V, May 1902. — 1 male, 10.7

× 7.6 (USNM 29380), Hilo, Hawaiian Island, Hawaii, United States, coll. H. Henshaw. — 7 males, 11.3 × 8.1 – 17.4 × 12.2, 4 females, 10.1 × 7.2 – 15.6 × 10.8 (USNM 1181365), Volcano House, Kilauea, Hawaii Island, Hawaii, United States, coll. O. Degener. — 2 males, 17.1 × 11.6 – 15.2 × 10.9, 2 females, 11.2 × 7.8 – 14.4 × 10.1 (USNM 99146), Nanakuli, Oahu Island, Hawaii, United States, coll. C. Cutress, 7 March 1950. — 1 female, 4.6 × 3.3 (UF 12408), Stn. FFS-0193, 23.8445° -166.3348°, 60 m, back reef, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 26 November 2006. — 1 female, 6.7 × 4.8 (UF 12368*), Stn. FFS-0157, 23.8705° -166.2843°, 0 m, intertidal sand, French Frigate Shoals, Hawaiian Islands, USA, coll. S. Godwin *et al.*, 22 October 2006. — 2 males, 10.2 × 7.6 – 12.3 × 8.8 (UF 12379), Stn. FFS-0086, 23.8732° -166.2348°, 4 m, reef crest, French Frigate Shoals, Hawaiian Islands, USA, coll. B. Zgliczynski *et al.*, 16 October 2006. — 1 female, 10.5 × 7.3 (UF 28762), Stn. Pittman-1110217.3, 3–8.5 m, rocky coast, Kamole III, Maui Island, Hawaiian Islands, USA, coll. C. Pittman, 17 February 2011. — 1 male, 5.0 × 3.8 (UF 12437*), Stn. Pittman-1070403, 21.0031° -156.6694°, 2–8 m, rocky coast, Maui, Kapalua Bay, Maui Island, Hawaiian Islands, USA, coll. C. Pittman, 3 April 2007.

Society Islands: 1 male, 18.65 × 12.88, 1 female, 15.54 × 10.86 (USNM 81438), 2412, Society Islands, coll. A. Garrett, 21 October 1864. — 2 males, 19.3 × 13.0 – 19.9 × 13.5, 1 female, 13.8 × 9.4, 3 ovigerous females, 15.3 × 10.5 – 16.8 × 11.4 (USNM 1181367) reef, W of Waroa Pass, Moorea, Society Islands, French Polynesia, coll. Bredin Expedition, 7 May 1957. — 1 female, 8.5 × 5.8, 2 juveniles (USNM 1181333), 1 m, SW end of Tetaro Island, Taoro Island, Raiatea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, W. Schmitt, 29 April 1957. — 1 male, 10.0 × 6.8 (USNM 1181289), off N end of Taoru Island, Raiatea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, W. Schmitt, 29 April 1957. — 1 female, 7.9 × 5.5 (USNM 1181362), shore, coral, sand flat E of protestant church, Uturoa, Raiatea, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 28 April 1957. — 6 males, 5.2 × 3.9 – 20.2 × 13.6 (USNM 1181305), 0–1 m, reef, N of Baie Fare and S of Point Teopape, off Point Teffaar, Huahine, Society Islands, French Polynesia, Bredin Pacific Expedition, 2 May 1957. — 1 female, 15.0 × 10.4 (USNM 1181304), outer reef in coral, Vaiorea Island, Society Islands, French Polynesia, coll. Bredin Pacific Expedition, 1 May 1957. — 1 female, 10.6 × 7.8 (UF 10097*), Stn. GP-Loc-862, -17.4964° -149.7528°, 0–1 m, under rock in 10–20cm sand in horizontal burrow, narrow oceanic reef flat, Narrow Reef Flat Around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon & G. Paulay, 20 June 2006. — 1 female, 15.4 × 10.7 (UF 9843*), Stn. GP-Loc-862, -17.4964° -149.7528°, 0–1 m, under rocks, narrow oceanic reef flat, Narrow Reef Flat Around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al*., 20 June 2006. — 1 female, 12.5 × 8.9 (UF 10090*), Stn. GP-Loc-862, -17.4964 -149.7528, 0–1 m, under rock in 10–20cm sand in horizontal burrow, narrow oceanic reef flat, Narrow Reef Flat Around Pt. Faupo, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon & G. Paulay, 20 June 2006. — 1 male, 14.9 × 10.3 (UF 15957*), Stn. MIB_108, -17.4902° -149.826°, 0–2 m, coral heads near outer reef, silty fringing reef in bay, Gump reef and barrier, Moorea Island, Society Islands, French Polynesia, coll. J. Poupin, 22 October 2008.

Tuamotu Islands: 1 male, 10.00 × 6.95, 1 female (UF 1613*), BRNG-032, -14.9833° -147.6167, outer reef flat, and reef crest, nestled in crevices in reef rock, Avatoru Motu, off Far W Hoa, Tuamotu Islands, French Polynesia, coll. G. Paulay, 30 October 2001. — 1 male, 18.24 × 12.57 (USNM 33269), Makemo, Tuamotus, coll. Bur. of Fisheries, 21 October 1899. — 1 male, 18.2 × 12.5 (USNM 33269), 16 35 S 143 40 W, reef, Makemo Island, Tuamotu

Archipelago, French Polynesia, coll. Albatross R/V, 21 October 1899. — 1 female, 19.0 × 13.0 (USNM 1181303), 3–5 m, in the vicinity of Mareva Anchorage, patch reef in lagoon S of deep water pass, Tikehau Atoll, Tuamotu Archipelago, French Polynesia, coll. Bredin Pacific Expedition, 12 April 1957. — 1 ovigerous female, 13.8 × 9.5 (USNM 95051), near shore, from under rocks etc., Homohomo Island, Raroia Atoll, Tuamotu Archipelago, French Polynesia, coll. J. Morrison, 21 July 1952. — 1 male, 11.0 × 7.8 (UF 18530), Stn. Bacchet-001, reef flat, Mekemo, Makemo Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, April 2009. — 1 female, 7.9 × 5.8 (UF 18539), Stn. Bacchet-002, reef flat, Niau, Niau Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, January 2009.

Diagnosis. Carapace (Pl. 28B) transversely hexagonal, ca. 1.4 broad as long; regions well defined, separated by deep furrows, covered with tomentum between numerous pearliform granules, 2M completely divided longitudinally, 3M tripartite, anterior margin reaching about half length of 2M, 1P laterally without setae and covered with conjoined pearliform granules. Frontal (Pl. 28C) submedian lobes convex, margin lined with granules, separated by wide U-shaped notch; lateral lobes small, rounded, granulate. Anterolateral margin with four lobular, granulate teeth excluding outer supraorbital tooth; margins sometimes with conical granules. Anterolateral angle of basal antennal segment expanded, forming flange, completely or incompletely blocking orbital hiatus. Pterygostomial region minutely granulate, without setae mesially, covered with thick, long, plumose setae diagonally along posterior, lateral surface, sometimes sparse. External surface of third maxilliped merus, carpus, propodus covered in tomentum; anterior margin of merus with deep notch. Chelipeds (Pl. 28E, F) unequal, external surfaces covered in minute tomentum; external surface of carpus with raised clusters of pearliform granules, one or two furrows parallel to articulation with propodus; external surface of chela with large pearliform or conical granules, proximally covered with tomentum, inferior surface smooth; pigmentation of fixed finger proximally extending 1/2 distance of external surface, greater than 3/4 distance inferior surface. Ambulatory legs (Pl. 28A) stout, external surface covered in tomentum and scattered granules, extensor margin lined with stout spines and thick fringe of long, plumose setae; tip of dactylus with long pigmented spine. Male thoracic sternum (Pl. 28D) minutely granular, posteriorly covered with tomentum. Male abdomen (Pl. 28D) moderately stout; somites 1, 2 covered with tomentum; somites 3 to 5 laterally covered with tomentum; somite 6 approximately as broad as long; telson ca. broad as long. G1 (Pl. 43A) distally bent ventroposteriorly with long, plumose setae, tip spatulate, longitudinally hollowed.

Remarks. This species is common and well represented in literature and museum collections. Several junior synonyms were noted by Clark and Galil (1993): *Xantho dehaanii* Krauss, 1834 by Miers (1884); *Chlorodius perlatus* MacLeay, 1838 by A. Milne Edwards (1873); *Etisodes caelatus* Dana, 1852 by Haswell (1882); *Actaeodes affinis* Dana, 1852 (assigned to *Actaea* by A. Milne Edwards) by Montgomery (1931); and *Actaea perlatus* MacLeay, 1838 and *Chlorodopsis areolatus brandonensis* Ward, 1942 by Barnard (1950). The holotype specimen from Australia is not extant. Clark & Galil (1993, pp. 1125–1127) clarified the taxonomy of this species. *Pilodius areolatus* is easily distinguished from its congeners in having well-defined, bulging carapace regions separated by deep furrows and covered in thick tomentum and pearliform granules, a quadrilobate anterolateral margin without emergent spines, and a distinct G1 (Pls 28B, 43A). As noted by Forest & Guinot (1961: 93), the anterolateral flange of the basal antennal segment in *P. areolatus* does not completely block the orbital hiatus. *Pilodius* *areolatus* and *P. miersi* are the only *Pilodius* species without a fully blocked orbital hiatus.

Distribution. *Pilodius areolatus* is reported from the Red Sea and South Africa throughout tropical Indo west-Pacific to Hawaii. It has also been collected as far south as just north of Sydney, Australia (Pl. 51A).

Pilodius granulatus Stimpson, 1859

Pls (29, 43B, 51C)

Pilodius granulatus Stimpson 1859: 34; 1907: 58, pl. VII, fig. 2 [Hong Kong]. — Serène 1968: 80 [List]. — Garth & Kim 1983: 685 [Jolo I., Philippines]. — Clark & Galil 1993: 1133, figs 5A–G, 33A, 41B [Hong Kong; Singapore; Gulf of Davao and Palawan, Philippines; Palau; Pulau Soegi and Pulau Sakit, Indonesia; Arafura Sea; Lizard I. and Port Darwin, Australia].

Chlorodopsis granulatus Miers 1884: 216 (part), plate XXI, fig. a [Port Darwin, Port Denison, and Port Molle, Australia].

Chlorodopsis philippinensis Ward 1941: 11 [Gulf of Davao, Philippines].

Pilodius serènei Miyake & Takeda 1968: 393, figs 3, 4 [Palau]. — Serène 1968: 80 [List]. — Takeda & Nunomura 1976: 62, 73 [Locality Uncertain].

Material examined. *Philippines:* 1 paratype male, 9.19 x 6.11, 1 paratype ovigerous female, 7.37 x 5.11 (AMNH 8319), Padada Beach, Gulf of Davao, Philippines, G. Oesch, June 28, 1936. — 1 female, 8.81 x 6.41, 1 ovigerous female, 8.78 x 6.02 (AMNH 8298), Padada Beach, Gulf of Davao, Philippines, G. Oesch, July 6. — 1 ovigerous female, 7.46 x 5.32 (AMNH 8376). — 1 male, 9.2 × 6.2 (AMNH 18521), Padada Beach, Gulf of Davao, Philippines, coll. G. Oesch, September, 1939. — 1 female, 9.65 × 6.45 (ZRC

2013.0737*), Stn. B8, 3 m, 9°37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, Panglao Expedition 2004, coll. 7 June 2004. — 1 male, 8.95 × 6.25 (ZRC 2013.0733), Stn. D12, 2–4 m, 9°38.5'N 123°51.0'E, mud, Panglao channel, Tagbilaran, coll. Panglao Expedition, 28 June 2004.

Indonesia: 4 males, 7.3 × 4.9 – 11.50 × 7.45, 4 females, 5.2 × 3.4 – 7.5 × 4.9, 2 ovigerous females, 7.7 × 5.1 – 8.5 × 5.6 (ZRC 1999.0379*), Tondang, Tanjung, Pulau Bintan, Riau Archipelago, Indonesia, coll. P. Ng, honours class 1995. — 13 males, 7.3 × 4.9 – 10.0 × 6.8 (ZRC 1969.11.24.16–19), Pulau Sakit, Indonesia, coll. R. Serène, 1963.

Thailand: 3 males, 3.5 × 2.4 – 7.6 × 5.0, 5 females, 5.3 × 3.6 – 8.4 × 5.5 (USNM 1181387), 2 m, Koh Kahdat, Thailand, Gulf of Thailand, coll. T. Mortensen, the Mortensen Siam Expedition 1899-1900, Jan 1900 to Feb 1900.

Singapore: 5 males 6.7 × 4.6 – 11.90 × 8.00 (ZRC 1989.3436–3440) Sentosa Reefs, Singapore, coll. P. Ng, 13 December 1989. — 1 female, 11.6 × 7.5 (ZRC 1999.0287*), Cyrene Reefs, Singapore, coll. D. Yeo & S. H. Tan, 19 May 1999. — 1 male, 10.8 × 6.9, 1 female, 11.8 × 7.6 (ZRC 2013.1642), SGBR_0006, 0-30 cm, hand, low tide, rubble, under rocks, old, dead coral rubble, rocks, mudflat, man-made breakers (boulders), reef in front of first mangrove right of boat drop-off, Semakau, Singapore, coll. 2011. — 1 male, 12.3 × 8.3 (ZRC 2013.1643*), SGBR_0004, 0-30 cm, hand, low tide, rubble, under rocks, old, dead coral rubble, rocks, mudflat, man-made breakers (boulders), reef in front of first mangrove right of boat drop-off, Semakau, Singapore, coll. 2011. — 5 males, 8.6 × 5.8 – 11.4 × 7.4, 3 females, 7.2 × 4.8 – 9.2 × 6.1, 1 ovigerous female, 8.8 × 5.8 (ZRC 1965.11.11.110-118), Pulau Ubin, Singapore, coll. M. Tweedie, June 1934. — 2 males, 9.5 × 6.2 – 10.4 × 6.7, 1 female, 10.2 × 6.6 (ZRC 1985.1503-1505), Sentosa Reef, Singapore, coll. 27 May 1982. — 1 male, 7.7 × 5.1, 2 ovigerous females, 8.2 × 5.6 – 8.8

× 5.5 (UF 36180*), Stn. SW12, 1.2186° 103.85131667°, 0–1 m, sandy bottom with rocks, St John's Island, DRTech, north lagoon, Singapore, coll. A. Anker, 21 May 2013. — 1 male, 10.9 × 7.3 (UF 36195*), Stn. SW27, 1.21518333° 103.85118333°, 0–5 m, St John's Island, DRTech, along seawall at south lagoon, Singapore, coll. N. Evans, 22 May 2013.

Australia: 1 male, 12.6 × 8.3 (UF 17011*), AUST-1017, AUST-ST-046, 0–1 m, -14.7747° 145.3673°, under rocks, reef flat, Martin Reef, W of Lizard Island, Queensland, Australia, coll. R. Lasley & F. Michonneau, 16 February 2009. — 1 female, 8.8 × 6.0 (UF 17123*), AUST-1179, AUST-ST-046, 2-3 m, -14.7746° 145.3673°, dead when preserved, rubble, reef flat, Martin Reef, W of Lizard Island, Queensland, Australia, coll. C. Watson, 16 February 2009.

Vanuatu: 1 male, 8.4 × 5.8 (ZRC 2013.1644), Stn. VM53, intertidal, 15°31'S, 167°11.9'E, soft and hard bottom, Segond Channel, vicinity of Luganville, Vanuatu, coll. Santo Marine Biodiversity Survey, 06 October 2006.

Diagnosis. Carapace (Pl. 29B) transversely hexagonal, ca. 1.5 broad as long, surface covered with light-colored tomentum; regions well defined, separated by deep furrows, 2M completely or incompletely divided longitudinally, 3M entire. Frontal (Pl. 29C) submedian lobes convex or straight, margin lined with granules, separated V- or U-shaped notch; lateral lobes projecting or confluent with submedian lobes, triangular or rounded, granular. Anterolateral margin with four multispinose lobes tipped with emergent, curved, anteriorly-directed spine. Anterolateral angle of basal antennal segment expanded, forming flange, completely blocking orbital hiatus. Pterygostomial region minutely granulate, with lateral and posterior short, plumose setae. External surface of third maxilliped granulate, without setae (sometimes sparse almost indiscernible tomentum on merus); anterior margin of merus relatively straight before convex junction with carpus. Chelipeds (Pl. 29E, F) unequal, granulate, tomentose; anterior margin of merus lined with spines; superior surface of carpus covered with large conical granules; external surface of chela with large conical granules, proximal tomentum, inferior surface smooth; pigmentation of fixed finger extending proximally 2/3 distance of inferior surface, 1/3 distance of external surface. Ambulatory legs (Pl. 29A) moderately stout, with long plumose and simple setae especially on extensor margin; extensor margin of merus lined with short spines; tip of dactylus with long pigmented spine, slightly longer than subdistal non-pigmented spine. Male thoracic sternum (Pl. 29D) granulate, sometimes with few, long posterior setae; S4 sometimes with short pubescence. Male abdomen (Pl. 29D) long, stout, with long, plumose, posterior setae; somite 6 ca. broad as long; telson slightly longer than broad. G1 (Pl. 43B) with short, stout subdistal setae and spines; apical lobe slightly reflexed or strongly twisted and directed laterally.

Remarks. Stimpson (1859: 34) gave a short description of *Pilodius granulatus* without mentioning the pigmentation of the male chelae, an important character for distinguishing *P. granulatus* and *P. miersi*. Apparently, Stimpson had examined some specimens with dark pigmentation completely encompassing the male chelae and some with dark pigmentation restricted to the inferior half. In his later, lengthier, description of the *P. granulatus*, Stimpson (1907: 58, pl. VII, fig. 2) described the species with encompassing pigmentation but illustrated a specimen with pigmentation restricted to the inferior surface. Confusion ensued. Miers (1884: 216) indicated that the pigmentation is intraspecific variation. Subsequently, Ward (1936: 4) described *P. miersi* in a couple sentences without mentioning chelae pigmentation in the new species. He did mention, however, that pigmentation in *P. granulatus* “almost covers the whole surface” of the palm. This seems to indicate that in *P. granulatus*, the pigmentation encompasses the whole chela, whereas in *P. miersi*, the pigmentation is restricted to the inferior half of the chelae. Sakai (1936, 1939, 1965, 1976), Dai, Yang, Song and Chen (1986), Dai and Yang (1991), and Serène and Luom (1959) seem to have thought so as well, as they figured or described specimens with this encompassing pigmentation under the name *P. granulatus*. However, Clark & Galil (1993: 1138) examined Ward's (1936) type material of *P. miersi* and indicated that the specimens have chelae with encompassing pigmentation. Clark & Galil (1993) also stated that Stimpson's (1859) original description refers to specimens without the encompassing dark pigmentation. This decision is counter to Stimpson's (1907) textual description, but agrees with his figure. Furthermore, their decision agrees with Ward's (1936) holotypes of *P. miersi*, which Clark & Galil (1993) examined, but disagrees with Ward's (1936) written comparison between *P. miersi* and *P. granulatus.* In short, *P. granulatus* has male chelae with dark pigmentation restricted to the inferior half of the chelae, whereas *P. miersi* has male chelae with encompassing dark pigmentation (Pls 29E, F, 31E, F).

Clark and Galil (1993: 1135) sank two synonyms of *Pilodius granulatus* (*Chlorodopsis philippinensis* Ward, 1936 and *Pilodius serènei* Miyake & Takeda, 1968) without commenting on their decision, leading to confusion due to the variation in the direction and curvature of the G1 tip. Davie (2005: 158) reviewed the decision by Clark & Galil (1993) and came to the conclusion, based on differences in the angle and direction of the "apical tongue" of the G1 in certain specimens, that there are two distinct species: *P. philippinensis* and *P. granulatus*. However, examination of numerous specimens has revealed that the differences in G1 tips amount to intraspecific variation, with specimens possessing, in Davie's (2005) language, an "apical tongue strongly twisted and directed laterally" (ZRC 2013.0733*), intermediate (ZRC 1989.3436–3440), and an "apical tongue slightly reflexed but still directed distally" (ZRC 1969.11.22.7–16). Some lots (e.g., USNM

1181378) contain specimens with both G1 forms. Therefore, *P. philippinensis* is regarded as a junior synonym of *P. granulatus*.

Pilodius granulatus is similar to *P. miersi*, *P. maotieni*, *P. moranti*, *P. pilumnoides* and *P. nigrocrinitus* in general shape of the carapace and anterolateral teeth, chelae and ambulatory legs, and setation of the carapace. Although, these species have distinct G1s. However, *Pilodius granulatus* is most similar to *P. miersi* in size and having low plumose tomentum covering the carapace (versus short, stout bristles in *P. nigrocrinitus*, *P. pilumnoides*, *P. moranti* and *P. moatieni*). However, they differ in pigmentation of the male chelae (see above). The tomentum of the carapace is usually present, but is sometimes almost completely absent (e.g., UF 17011).

Distribution. The geographic range of *P. granulatus* is restricted to the Coral Triangle and adjacent areas such as the Great Barrier Reef and Vanuatu (Pl. 51C).

Pilodius maotieni Serène, 1971

Pls (30, 43C, 51D)

Chlorodopsis pilumnoides, Serène and Luom 1958: 102 (part), pl. IC, IIIa, IVB [Vietnam]; 1959: 302 (part), fig. 2A, 5G, pl. 3A [Vietnam]. [not *Pilodius pilumnoides* (White, 1848)]

Pilodius maotieni Serène 1971: 913 [Nha Trang, Vietnam]; 1984: 238, fig. 152 [Vietnam]. — Clark & Galil 1993: 1135, figs 6A–G, 33B, 41C [Nha Trang, Vietnam; Indochina; Macclesfield Bank; Pearl Bank, Philippines; Lagon Nord, New Caledonia].

Material examined. *Vietnam:* 1 holotype male, 17.2 × 11.6 (MNHN 9313), Nha Trang Bay, Vietnam, coll. R. Serène, 1957.

Philippines: 1 female, 8.1 × 5.7 (USNM 65284), 14 05 05 N 120 19 45 E, W of Fortune Island, Luzon Island, Cavite, Philippines, coll. United States Fish Commission, Philippines Expedition, Albatross R/V, 15 January 1908.

Australia: 1 male, 13.0 × 9.1 (UF 18145*), AUST-2017, AUST-ST- , -14.4544° 145.5043°, in dead *Pocillopora*, Hicks Reef, Lizard Island, Queensland, Australia, coll. M. Timmers, 14 February 2009. — 1 female, 16.2 × 10.9 (UF 18355*), AUST-2462, -14.6926° 145.4684°, in dead *Pocillopora*, SE Lizard Island, Bird Island, Queensland, Australia, coll. M. Timmers, 23 February 2009.

Papua New Guinea: 1 male, 23.7 × 15.5 (UF 2631*), GP-Loc-553-2, 18–22 m, -10.7253° 151.7423°, from *Holothuria* aff. *atra*, NNW corner off Gabugabutau Islet, Conflict Atoll, Louisade Archipelago, Milne Bay Province, Papua New Guinea, coll. G. Paulay, 29 May 1998.

Mariana Islands: 1 male, 12.2 × 8.7 (UF 997*), ZZZ-016626, 18 m, 13.5968° 144.8317°, under loose rubble, fore reef, Haputo, Guam Island, Mariana Islands, coll. L. Kirkendale, 17 May 2001. — 1 female, 12.1 × 8.2 (UF 1298*), ZZZ-085739, 5–90 ft, under or among rocks, near harbor entrance, Glass Breakwater, Apra Harbor, Guam Island, Mariana Islands, coll. H. Conley, 22 August 1984.

Vanuatu: 1 male, 19.8 × 13.1, 1 female, 15.0 × 10.5 (ZRC 2013.1645*), Stn. DB71, 7 m, 15°21.6’S, 167°12.5’E, massive coral, S Turtle Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 27 September 2006. — 1 female, 14.8 × 10.0 (ZRC 2013.1646*), Stn. DB58, 6-43 m, 15°24.6’S, 167°14.3’E, sand and corals, Aésé Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 23 September 2006.

Diagnosis. Carapace (Pl. 30B) transversely hexagonal, ca. 1.5 broad as long; surface granulate, granules robust, pearliform medially, larger and conical laterally; regions well defined, separated by deep, smooth furrows, covered in short, stout, simple, dark setae and fewer long plumose setae; 2M completely divided longitudinally, 3M entire. Frontal (Pl. 30C) submedian lobes convex, margin lined with granules, separated by U-shaped notch; lateral lobes triangular or rounded, granulate. Anterolateral margin with four multispinose lobes tipped with emergent, curved, anteriorly-directed, robust spine. Anterolateral angle of basal antennal segment expanded, forming flange, completely blocking orbital hiatus. Pterygostomial region minutely granulate, with mesial minute dark setae; with plumose setae diagonally from posterior to lateral surface, sometimes absent in small specimens. External surface of third maxilliped granulate, covered with minute, dark setae; anterior margin of merus nearly straight with small notch before convex junction with carpus. Chelipeds (Pl. 30E, F) subequal, covered with short, dark, plumose setae and robust conical granules; merus stout, anterior margin lined with spines; pigmentation of fixed finger of male chelae extending proximally 1/2 distance of inferior surface, less than 1/3 distance external surface; inferior surface of chelae smooth. Ambulatory legs (Pl. 30A) stout, covered in short, dark, simple setae, and long, dark, plumose setae; extensor margin of merus lined with short, robust, dark, posteriorly directed spines; dactylo-propodal locking mechanism well developed; tip of dactylus with long pigmented spine, short subdistal spines. Male thoracic sternum (Pl. 30D) minutely granulate, covered with short, dark, simple setae, few long setae posteriorly. Male abdomen (Pl. 30D) stout, covered with short, dark, simple setae, few long setae; somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 43C) stout, ventrally curved distally; with numerous long, stout subdistal setae; apical lobe spatulate, angled 90 degrees.

Remarks. *Pilodius maotieni* was described relatively recently by Serène (1971) for specimens reported as *P. pilumnoides* by Serène & Luom (1958, 1959). Serène (1971) differentiated between these two species based on the morphology of their G1s. *Pilodius maotieni* has a G1 with a relatively short, broad apical lobe (Pl. 43C) [versus thin and elongate in *P. pilumnoides* (Pl. 44C)]. These two species are also similar to *P. nigrocrinitus* in shape and setation of the carapace (Pls 30B, 33B, 34B). However, the male sterna of *P. maotieni* and *P. pilumnoides* are generally covered with short dark setae (versus absent in *P. nigrocrinitus*). Although, this character should be used with caution, as the setae is sometimes removed by abrasion and/or with age. Also, Clark & Galil's (1993) key to the species of *Pilodius* indicates that *P. maotieni* specimens have cheliped meri with granulate anterior margins, though the margin in many specimens is granulate (e.g., UF 2631, UF 18145, UF 997, ZRC 2013.1645).

Distribution. This species is recorded from the Coral Triangle and adjacent areas such as Vietnam, the Great Barrier Reef, Guam, and Vanuatu (Pl. 51D).

Pilodius miersi (Ward, 1936)

Pls (31, 43D, 52A)

Chlorodopsis miersi Ward, 1936: 4, pl. II, figs 1-3 [type locality = Singapore and Lindeman Island, Australia].

Chlorodopsis granulatus, Miers 1884: 216 (part), pl. XXI, fig. A [Port Molle, Australia]. — Sakai 1956: 40 (Appendix). (non *Pilodius granulatus* Stimpson, 1859)

Chlorodopsis granulata, Sakai 1935: 164, pl. 49, fig. 1 [Japan]; 1939: 503, Text-fig. 41, pl. LXII, fig. 1, pl. XCVII, fig. 6 [Harbor of Simoda, Japan]. — Serène and Luom 1959: 307, fig. lA, fig. 2E, F, pl. I fig. D, pl. III fig. C, F [Vietnam]. (not *Pilodius granulatus* Stimpson, 1859)

Pilodius granulatus, Sakai 1965: 148, pl. 73, fig. 6 [Sagami Bay, Japan]; 1976: 460, pl. 164, fig. 3 [Sagami Bay, Shimoda, Kii Nagashima, Kii Minabe, and Yoron I., Japan]. — Dai *et al.* 1986: 306, pl. 43(3), fig. 165(B) [Review]. — Dai & Yang 1991: 329, pl. 43(3), fig. 165B(2) [Review]. (not *Pilodius granulatus* Stimpson, 1859)

Pilodius miersi Serène 1968: 80 [List]. — Clark & Galil 1993: 1136, figs 7A–G, 34A, 41D [Kushimoto and Magari-Zaki(?), Japan; Vietnam; Singapore; Luzon, Jolo I. and Tinakta, Philippines; Magnetic I., Hayman I., Lindeman I., Porto Molle, Seaforth I., Australia].

Pilodius luomi Serène 1971: 913 [Horsbourg Lighthouse, Singapore]; 1984: 240 [Key].

Material examined. *Philippines:* 1 male, 6.7 × 4.6 (ZRC 2013.0732*), Stn. B12, 24–27 m, 9°35.6'N 123°43.2'E, reef slope, Doljo point, Panglao Island, 14 June 2004. — 1 male, 10.7 × 7.2, 1 female, 9.0 × 6.0, 1 ovigerous female, 11.2 × 7.7 (USNM 65283), 38 m, 05 41 40 N 120 47 10 E, NW of Tapul Island, Tapul Group, Sulu, Philippines, coll. United States Fish Commission, Philippines Expedition, Albatross R/V, 16 February 1908. — 2 males, 6.1 × 4.2 – 6.9 × 4.5 (USNM 1181201), 06 03 45 N 120 57 0 E, Candea Point, Jolo Island, Sulu, Philippines, coll. United States Fish Commission, Philippines Expedition, 5 March 1908. — 2 males, 8.1 × 5.3 – 8.6 × 5.8, 1 female, 7.7 × 5.4 (USNM 65290), 18 m, 5 11 50 N 119 54 00 E, Tinakta Island, Tataan Passage, Tawitawi Island, Tawitawi Group, Sulu

Archipelago, Philippines, United States Fish Commission, Philippines Expedition, Albatross R/V, 21 February 1908.

Japan: 2 males, 5.2 × 3.8 – 11.3 × 7.7 (ZRC 2013.1648), man-made beach beside ferry port at Sakurajima, Kagoshima, Japan, coll. P. Ng & T. Naruse, 25 October 2011.

Australia: 1 male, 10.6 × 7.0 (UF 25804*), AUST-6362, HI09-106, 30 m, -23.4541° 151.9168°, in rubble, Heron Island, Queensland, Australia, coll. F. Michonneau & S. McKeon, 25 November 2009. — 1 male, 14.6 × 9.1 (USNM 78428), coral reefs, Lindeman Island, Queensland, Australia. — 1 male, 7.1 × 4.6 (UF 24734*), Stn. HI09-007, -23.4321333° 151.93375°, in rubble, back reef, Heron Island, First Point, North Heron Reef, Queensland, Australia, coll. 12 November 2009. — 1 ovigerous female, 7.5 × 4.9 (UF 24758*), Stn. HI09-010, -23.43321667° 151.93375°, 8–10 m, in rubble, back reef, bommies on sand, *Acropora* patches, Heron Island, First Point, North Heron Reef, Queensland, Australia, coll. 12 November 2009. — 1 female, 8.6 × 5.6 (UF 25142*), Stn. HI09-038, -23.28551667° 151.76695°, Heron Island, Queensland, Australia, coll. 17 November 2009. — 1 male, 10.0 × 6.7 (UF 25930*), Stn. HI09-122, -23.4727667° 151.96°, 15–19 m, Heron Island, Queensland, Australia, coll. S. Smith *et al.*, 28 November 2009. — 1 ovigerous female, 8.4 × 5.6 (UF 17475*), Stn. AUST-ST-088, -14.6706° 145.5674°, 25–30 m, coral rubble, fore reef, Lizard Island, Snake Pit station 1, Queensland, Australia, coll. S. Smith *et al.*, 24 February 2009.

Papua New Guinea: 1 male, 9.0 × 6.1 (UF 3857*), Stn. GP-Loc-561, -11.1025° 152.471667°, 40 m, under rubble, Louisiade Archipelago, Vegetated Low Island Northwest of Migemma Gemma Pass, Western Calvados, Milne Bay Province, Papua New Guinea, coll. G. Paulay, 2 June 1998.

Diagnosis. Carapace (Pl. 31B) transversely hexagonal, ca. 1.5 broad as long; surface covered with light-colored tomentum; regions well defined, separated by deep furrows; 2M completely or incompletely divided longitudinally, with anterior tuft of long, plumose setae; 3M entire or divided; 5L with anterior tuft of long, plumose setae. Frontal (Pl. 31C) submedian lobes convex, margin lined with granules, separated V- or U-shaped notch; lateral lobes triangular, granular. Anterolateral margin with four multispinose lobes tipped with emergent, curved, anteriorly-directed spine. Anterolateral angle of basal antennal segment expanded, forming flange, completely or incompletely blocking orbital hiatus. Pterygostomial region minutely granulate. External surface of third maxilliped granulate, sometimes covered in tomentum; anterior margin of merus straight or slightly concave before convex junction with carpus. Chelipeds (Pl. 31E, F) unequal, granulate, covered with short, light-colored tomentum; merus stout, anterior margin lined with spines, short tomentum; superior surface of carpus with robust conical granules; external surface of chelae large with robust conical granules, inferior surface smooth; pigmentation of male chelae encompassing propodus. Ambulatory legs (Pl. 31A) moderately stout, covered in short, light-colored tomentum, extensor margins fringed with long plumose setae; extensor margin of merus lined with short spines; dactylo-propodal locking mechanism well developed; tip of dactylus with long pigmented spine, short non-pigmented spine. Male thoracic sternum (Pl. 31D) granulate, posteriorly with short tomentum. Male abdomen (Pl. 31D) stout, posteriorly covered with short tomentum; somite 6 broader than long; telson large, ca. as broad as long. G1 (Pl. 43D) with stout, arched; subdistally fringed with long, stout setae; apical lobe ovate.

Remarks. Male specimens of *Pilodius miersi* are immediately recognizable by the pigmentation of the chelae, which encompasses the propodus (Pl. 31E, F). Clark & Galil (1993) synonymized *Pilodius luomi* Serène (1971) with *P. miersi* and clarified the confusion between *P. miersi* and *P. granulatus* in the literature (see remarks for *P. granulatus*). The two are the only *Pilodius* species covered in short, light-colored pubescence (Pls 29B, 31B). The carapace of *Pilodius miersi* is generally more setose than that of *P. granulatus*, and the ambulatory legs are generally more thickly fringed with setae. Although, setation is sometimes absent, likely due to abrasion and/or age.

Distribution. This species is restricted to the Coral Triangle and adjacent areas such as Japan and the Great Barrier Reef (Pl. 52A).

Pilodius moranti Clark & Galil, 1993

Pls (32, 44A, 52B)

Pilodius moranti Clark & Galil 1993: 1138, figs 8A–D, 34B, 42A [Type Locality = NE coast of Australia?; Porpoise Cay, Lord Howe I., and Middleton Reef, Australia].

Material examined. *Australia:* 4 males, 8.8 × 6.7 — 16.9 × 11.6 (QM 15456), outer reef flat under dead coral boulders at low tide, Wreck Reef, nr Porpoise Cay, coll. J. Short & S. Mullens, 14 May 1988. — 1 female, 22.7 × 15.1 (QM 15455), outer reef flat under dead coral boulders and at base of live coral heads, Wreck Reef, nr Porpoise Cay, coll. J. Short & S. Mullens, 14 May 1988. — 1 male, 14.7 × 9.9 (QM 15143*), outer reef flat under dead coral boulders, low tide, Wreck Reef, nr Porpoise Cay, coll. J. Short & S. Mullens, 14 May 1988. — 1 male, 21.0 × 14.3 (QM 15454*), under dead coral boulders on coral rubble and sand, 0.5 m, Porpoise Cay, Wreck Reef, Coral Sea, coll. J. Short & S. Mullens, 10 May 1988. — 2 females, 13.8 × 9.2 – 18.8 × 12.6

(QM 15142*), outer reef flat under dead coral boulders at low tide, Wreck Reef, nr Porpoise Cay, coll. J. Short & S. Mullens, 14 May 1988.

Diagnosis. Carapace (Pl. 32B) transversely hexagonal, ca. 1.5 broad as long; surface granulate, granules conical laterally; regions well defined, separated by deep, smooth furrows, covered in short, stout, simple, dark setae, less numerous long setae; 2M divided longitudinally, 3M entire. Frontal (Pl. 32C) submedian lobes convex, margin lined with granules, separated by narrow U-shaped notch; lateral lobes triangular or rounded, granulate. Anterolateral margin with four multispinose lobes; spines curved, anteriorly directed; teeth 2, 3 largest with 3-4 spines of ca. equal size. Anterolateral angle of basal antennal segment slightly expanded forming small flange, incompletely blocking orbital hiatus. Pterygostomial region minutely granulate with long, plumose setae diagonally from posterior to lateral surface, sometimes absent in small specimens. External surface of third maxilliped granulate, merus covered with minute, dark setae, sometimes absent in small specimens; anterior margin of merus nearly straight with small indention before convex junction with carpus. Chelipeds (Pl. 32E, F) subequal, covered with short, dark, plumose setae, few scattered long setae, and robust, short conical granules; merus stout, anterior margin lined with spines, with transverse setae-fringed furrow near border with carpus; carpus with transverse, setae-fringed furrows; dorsal surface of merus and carpus with granulate, raised, setae-fringed regions; pigmentation of male propodus restricted to fixed finger; inferior surface of chelae smooth. Ambulatory legs (Pl. 32A) longitudinally flattened, covered in short, dark, simple setae; long, dark, plumose setae fringing extensor margin; extensor margin of merus lined with posteriorly directed spines; carpus and propodus with longitudinal, setae-fringed groove; dactylo-propodal locking mechanism well developed; tip of dactylus with long pigmented spine, short subdistal spine(s). Male thoracic sternum (Pl. 32D) minutely granulate, with short setae posteriorly, few scattered long setae. Male abdomen (Pl. 32D) moderately stout, covered with short, simple setae posteriorly and laterally; few long setae; somite 6 ca. broad as long; telson ca. as broad as long. G1 (Pl. 44A) stout, distal 1/3 curved ventrally; with numerous long, thin subdistal setae, many subdistal spines; apical lobe spatulate, longitudinally and transversely curved; proximal, anterolateral edge projecting.

Remarks. *Pilodius moranti* is easily distinguished from other *Pilodius* species by transverse setae-fringed furrows of the cheliped carpus and longitudinal setae-fringed grooves of the ambulatory leg carpus and propodus. It is also unique in having a narrow distribution off the east coast of Australia. The G1 is similar to *P. areolatus* but differs in having a projecting anterolateral margin of the apical lobe (Pls 43A, 44A).

Distribution. *Pilodius moranti* has not been reported since its original description, where it was recorded off the east coast of Australia (Pl. 52B).

Pilodius nigrocrinitus Stimpson, 1859

Pls (33, 44B, 52C)

Pilodius nigrocrinitus Stimpson 1859: 34 [Simoda, Japan]; 1907: 58, pl. 7, fig. l a, b [Simoda, Japan]. — Balss 1938a: 57 [List]. — Forest & Guinot 1961: 89 [List]. — Sakai 1965: 148, pl. 73, fig. 5 [Sagami Bay, Japan]; 1976: pl. 164, fig. 2, text-figs. 248a–b [Sagami Bay, Kasajima(?), Mitohama, Izu Shimoda, Kii Nagashima, Kii Minabe, Ashizurizaki and Amami Group, Japan]. — Serène 1968: 80 [List]; 1984: 235 [Key]. — Dai *et al.* 1986: 307, pl. 43(5), fig. 166(2) [Review]. — McNeill, 1968: 73 (part) [Great Barrier Reef, Australia]. — Takeda & Nunomura 1976: 73 [Gizo, Solomon

Islands; Nou Vata (in the vicinity of Noumea), Ilot Maitre, Plum, Anse Vata (in the vicinity of Noumea), Ile des Pins, and Poum, New Caledonia]. — Dai & Yang 1991: 330, pl. 43(5), fig. 166(2) [Review]. — Clark & Galil 1993: 1139, figs 9A–G [Phuket, Thailand; Great Cocos I.; Perhentian Besar, Aor I., Pulau Pangkor Laut, Tioman, and Kelantan, Malaysia; Edam I., and Ternate, Indonesia; Murray I., Cape York, Masthead I., Holborn I. (?), Port Douglas, Lady Elliot I., Swain Reef, One Tree I., Beach Rock (?), Townsville, Low Isles, Batt Reef, Asterina Spit, Lindeman I., Orpheus I., Mt. Adolphus I., Lizard I., and Palfrey I., Australia; Peu, Solomon Is.; Noumea Harbour, Anse Vata, Ricaudy Reef, Namie Reef, Phare Amedee Reef, and l'ilot Maitre, New Caledonia; ?Samoa].

Chlorodopsis melanochirus A. Milne-Edwards 1873: 228, pl. VIII, fig. 5 [New Caledonia]. — Haswell 1882: 55 [Holborn I. (?), Darnley I., and Port Molle, Australia]. — Ortmann 1893: 471 [Fiji Is.; NE Papua New Guinea]; 1894b: 52 [Ambon I., Indonesia]. — ?Nobili 1899: 30 [New Caledonia]. — Stephenson *et al.* 1931: 59 [Low Isles, Australia]. — Ward 1932: 251 [North West Island, Australia].

Chlorodopsis melanochira De Man 1887b: 281 [Edam I., Ambon I., Indonesia]; 1892: 278 [Insel Enkhuize, Indonesia]; 1895: 520 [Aceh]; 1902: 624 [Ternate, Indonesia]; 1929a: 1 [Pulau Berhala, Malaysia]. — Alcock 1898: 168 [Andaman Islands, India]. — Edmondson 1933: 250 [Review]. — ?Balss 1938a: 59 [Florida Island and Talagi, Salomon Islands; Fiji Island; Molukken, Batjan; Singapore; Batavia]. — Serène and Luom 1958: 117, pls IIB, IIId, IVd [Vietnam]. — ?Sankarankutty 1962: 139 [S Andaman, India].

Chlorodopsis nigrocrinitus Urita 1926: 11 [Kagosima Prefecture, Japan].

Chlorodopsis nigrocrinita Sakai 1935: 163, pl. 49, fig. 2 [Japan]; 1939: 504, text-fig. 42, pl. LXII, fig. 2, XCVII, fig. 2 [Simoda, Japan]. — Tweedie

1950a: 92 [Aur Island, Malaysia]. — Sakai 1956: 40 (Appendix). — Guinot 1958: 179, fig. 24a, b [Figure]. — Serène and Luom 1958: 112, pls IIA, IIIe, IVe [Vietnam]; 1959: 304, figs 2B, 5B, pl. IA [Vietnam]. — Sakai 1960: 70, pl. 35, 2 [Review?].

Chlorodopsis pilumnoides, Sankarankutty 1962: 138, figs 38, 39 [Car Nicobar]. [not *Pilodius pilumnoides* (White, 1848)]

Pilodius melanochira Serène 1968: 80 [List].

Pilodius spinipes, McNeill 1968: 74. [not *Luniella spinipes* (Heller, 1861)]

(?) *Chlorodopsis nigrocrinita* Alcock 1898: 168 [Andaman Islands].

Material examined. *Thailand:* 2 males, 6.5 × 4.3 – 9.3 × 6.0, 1 damaged female (USNM 39771), 2 m, Koh Kahdat, Thailand, Gulf of Thailand, coll. T. Mortensen, Mortensen Siam Expedition 1899-1900, January 1900 to February 1900. — 7 males, 5.7 × 3.9 – 12.7 × 8.3, 5 females, 6.8 × 4.5 – 11.5 × 7.5 (USNM 184262), Marsden Square: 027, Phuket Island, Thailand, Andaman Sea, coll. Fifth Thai Danish Expedition, Gallardo R/V, 4 February 1966. — 1 male, 10.6 × 7.2 (USNM 184261), Marsden Square: 027, Phuket Island, Thailand, Andaman Sea, coll. Fifth Thai Danish Expedition, Gallardo R/V, 4 February 1966.

Malaysia: 1 male, 10.50 × 7.15, 3 females (ZRC 1999.0933), Paya Beach, P. Tioman, Malaysia, coll. P. Ng, 24 June 1999. — 6 males, 10.4 × 6.7 – 12.3 × 8.1, 4 females, 9.6 × 6.5 – 11.4 × 7.3, 1 ovigerous female, 8.9 × 6.2 (ZRC 1965.11.11.137-146), Aur Island, South China Sea, Malaysia, coll. M. Tweedie, 1938.

Singapore: 1 male, 7.1 × 4.7 (ZRC 1985.1785), Sentosa Reef, Singapore, coll. P. Ng, 26 May 1982.

Indonesia: 2 males, 10.7 × 7.3 – 12.60 × 7.60, 1 female, 9.3 × 6.5 (ZRC 2003.0554*), EA-JL04, off Selat Peninting, south-eastern coast of the

Niulwan Peninsula, Pulau Matak, Anambas, Indonesia, coll. J. Lai *et al*., 14 March 2002. — 1 male, 10.1 × 7.0 (ZRC 2013.1651), Stn. BL11-002, BALI-0008, 0-10 cm, -8.713480° 115.251575°, hand, intertidaling, under rock, hard exposed substrate with sandy patches, scattered coral, exposed (low tide), closest beach from Rama Villas, Sanur Beach, Bali, Indonesia, coll. 15 June 2011. — 1 male, 10.3 × 7.0 (ZRC 2013.1652*), Stn. BL11-010, BALI-0356, 5-? m, under rock, coral reef, sand, seagrass, rocky shore, Sombu, Wanci, Sulawesi, Indonesia, coll. 24 June 2011. — 1 male, 12.7 × 8.9, 1 ovigerous female, 12.2 × 7.9 (ZRC 2003.0555), Natuna, north east coast of Pulau Paryan, north west of Pulau Bungarah, coll. 17 March 2002. — 1 male, 13.3 × 8.9, 1 ovigerous female, 10.8 × 7.2 (USNM 32389), Polo Edam, Indonesia, coll. J. Brock, 1887.

Australia: 1 male, 10.0 × 6.8, 1 female, 11.0 × 7.2 (USNM 156069), Green Island, Great Barrier Reef, Queensland, Australia, coll. W. Bartos, 1944. — 1 male, 10.2 × 6.8 (UF 25666*), AUST- 6163, HI09-035, 0–1 m, -23.4418° 151.9004°, under rock, Heron Island, coll. 16 November 2009. — 1 male, 11.8 × 7.8 (UF 17075*), AUST-1112, AUST-ST-049, 0–1 m, -14.7429° 145.5143°, under rocks, reef flat, North Direction Island, S of Lizard Island, Queensland, Australia, coll. A. Anker & R. Lasley, 17 February 2009. — 1 male, 16.8 × 11.1 (UF 17017), Stn. AUST-ST-046, -14.7746° 145.3673°, 0–1 m, under rocks, reef flat, W of Lizard Island, Martin reef, Queensland, Australia, coll. R. Lasley & F. Michonneau, 16 February 2009. — 2 males, 16.3 × 10.6 – 18.1 × 11.7, 1 ovigerous female, 12.7 × 8.2 (UF17010), Stn. AUST-ST-047, -14.6068° 145.3506°, 0–1 m, under rocks, reef flat, W of Lizard Island, Linnett reef, Queensland, Australia, coll. R. Lasley & F. Michonneau, 16 February 2009.

Japan: 1 male, 13.6 × 8.7 (UF 27095), GUOK10-2996, 0–4 m, 26.2928° 127.9174°, very silty bay, shallow, campground, white beach, Okinawa, Japan, coll. N. Evans *et al.*, 18 July 2010. — 1 ovigerous female, 12.2 × 7.9 (UF 27086), Stn. GUOK10-St-076, 26.292824° 127.917392°, 0–4 m, shallow, very silty bay, Okinawa, White Beach, campground, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 18 July 2010. — 1 ovigerous female, 10.8 × 7.3 (UF 27097), Stn. GUOK10-St-076, 26.292824° 127.917392°, 0–4 m, shallow, very silty bay, Okinawa, White Beach, campground, Okinawa Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 18 July 2010.

Philippines: 1 male, 9.88 x 6.74 (AMNH 8564), Gulf of Davao, Philippines, coll. 18 November 1937. — 2 males, 9.7 × 6.5 – 9.9 × 6.8 (USNM 65280), Port Binanga, Subic Bay, Luzon Island, Zambales, Philippines, coll. Philippines Expedition, Albatross R/V, 8 January 1908.

Guam: (?) 2 females (largest = 9.7 × 6.9), 1 juvenile (ZRC 2000.0729), fore reef, SW of Orote Peninsula, coll. G. Paulay, 15–18 April 2000.

Papua New Guinea: 1 male, 15.6 × 10.2 (ZRC 1965.11.11.59), Samarai, Papua New Guinea.

Solomon Islands: 2 males, 7.8 × 5.2 – 9.7 × 6.8, 2 females, 7.6 × 5.4 – 8.7 × 6.1 (UF 3398*), ZZZ-087900, 3–5 ft, among dead coral and rocks, near JFK Island, Ghizo Islands, Solomon Islands, coll. H. Conley, 10 February 2002. — 1 male, 10.4 × 6.9 – 1 ovigerous female, 8.8 × 5.9 (UF 3331*), Stn. ZZZ-087901, 3–5 m, among rocks, Near Nusatupe Island, Ghizo Island, Solomon Islands, coll. H. Conley, 25 February 2002.

New Caledonia: 1 male, 15.5 × 10.2 (UF 18008*), Stn. NC09-St-6, -22.313203° 166.457452°, 0–1 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 10 March 2009. — 1 ovigerous female, 11.8 × 7.9 (UF 18017), Stn. NC09-St-5, -22.313203° 166.457452°, 2–3 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 8 March 2009. — 1 female, 11.4 ×

7.8 (UF 18011), Stn. NC09-St-6, -22.313203° 166.457452°, 0–1 m, under rock, fringing reef, Noumea, Ricaudy, Province Sud, New Caledonia, coll. F. Michonneau, 10 March 2009. — 2 males, 2 females (cotypes of *Chlorodopsis melanochira* A. Milne Edwards, 1873) (USNM 20293), New Caledonia, coll. M. Balansa.

Vanuatu: 2 males, 9.6 × 6.4 – 14.8 × 9.7, 1 ovigerous female, 9.4 × 6.2 (ZRC 2013.1649*), Stn. VM35, intertidal, 15°29.4'S, 167°15.2'E, soft bottom, Palikulo Peninsula, Vanuatu, coll., Santo Marine Biodiversity Survey, 24 September 2006. — 1 male, 12.4 × 8.3 (ZRC 2013.1650), Stn. AT52, 52-62 m, 15°31.5'S, 167°12.7'E, Segond Channel, Vanuatu, coll. Santo Marine Biodiversity Survey, 02 October 2006.

Diagnosis. Carapace (Pl. 33B) transversely hexagonal, ca. 1.5 broad as long; surface granulate, granules larger and conical laterally; regions well defined, separated by deep, smooth furrows, covered in short, stout, simple, dark setae and fewer long plumose setae; 2M completely divided longitudinally, 3M entire. Frontal (Pl. 33C) submedian lobes convex, margin lined with granules, separated U-shaped notch; lateral lobes triangular or rounded, granulate. Anterolateral margin with four multispinose lobes, spines short, curved, anteriorly-directed. Anterolateral angle of basal antennal segment expanded, forming flange, completely blocking orbital hiatus. Pterygostomial region minutely granulate, with plumose setae diagonally from posterior to lateral surface. External surface of third maxilliped granulate, with or without few, short setae; anterior margin of merus nearly straight with or without notch before convex junction with carpus. Chelipeds (Pl. 33E, F) subequal, covered with short and long dark, simple setae and conical granules; merus stout, anterior margin lined with spines; carpus spinose; dark pigmentation of fixed finger extending proximally greater than 3/4 distance of inferior surface, ca. 1/2 distance of external surface; inferior surface of chelae smooth. Ambulatory legs (Pl. 33A) stout, covered in short simple setae and long simple or plumose setae; extensor margin of merus lined with short spines; dactylo-propodal locking mechanism well developed; tip of dactylus with long pigmented spine, short subdistal spine. Male thoracic sternum (Pl. 33D) minutely granulate, sometimes with few long setae posteriorly. Male abdomen (Pl. 33D) stout, posterior somites setose; somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 44B) moderately stout, distal 1/4 curved ventrally, twisted; with numerous stout subdistal setae; apical lobe hooked.

Remarks. *Pilodius nigrocrinitus* is similar to *P. maotieni* and *P. pilumnoides* in carapace shape, possessing stout black setae on the carapace, and similar anterolateral margins with four multispinose teeth (Pls 30B, 33B, 34B). However, *P. nigrocrinitus* differs from *P. pilumnoides* in possessing long, plumose setae on the carapace along with being covered with short, stout, dark setae (versus without long plumose setae in *P. pilumnoides*). It is also a much smaller species, measuring ca. 1–2 cm in carapace width (versus several cm in *P. pilumnoides*). *Pilodius nigrocrinitus* differs from *P. maotieni* in having a male thoracic sternum that is generally free of short, dark setae (versus covered in short dark setae in *P. maotieni*). Balss (1938) sank *Chlorodopsis melanochirus* A. Milne-Edwards, 1873 into *P. nigrocrinitus*, and Clark & Galil (1993) summarized the taxonomic history of the species.

Distribution. The record from Hawaii (Edmondson 1946: 296) is likely incorrect. Edmondson stated that the specimen looked like *P. nigrocrinitus*. However, based on his short description of the specimen (esp. the carapace having dense short and sparse long yellow setae), it is likely the specimen is *Soliella flava* comb. nov. All other records are from the Coral Triangle, and adjacent areas such as Thailand, New Caledonia, and Vanuatu (Pl. 52C).

Pilodius pilumnoides (White, 1848)

Pls (34, 44C, 51B)

Chlorodius pilumnoides White 1847: 18 (*nomen nudum*) [List]; White 1848a: 226 [Singapore; Bohol]; 1848b: 286 [Singapore; Bohol, Philippines]. — Adams & White 1849: 41, tab. IX, fig. 3 [Singapore; Philippines].

Chlorodopsis pilumnoides De Man 1887a: 35, 1887b: 281 [Ambon Island, Indonesia]. — Cano 1889: 204 [?]. — Alcock 1898: 167 [Andaman Islands, India; Mergui Archipelago, Myanmar]. — ?Ortmann 1893: 470 [Amami Oshima, Japan; Samoan Is.; Male Atoll, Maldives]. — Lanchester 1900: 737 [Singapore; Malacca, Malaysia]. — Rathbun 1923: 108 [SE of Cape Capricorn, Australia]. — McNeill 1926: 309 [North-West I., Australia]. — Gordon 1934: 47, fig. 26a [Banda Neira, Indonesia]. — Miyake 1936: 509 [Yaeyama, Japan]. — Balss 1938a: 59, pl. 1, fig. 4 [Viti Levu and Namuka, and Kandavu, Fiji; Timor, Indonesia; Cape York; New Britain]; 1938b: 56 [Singapore]. — Sakai 1939: 505, text-fig. 43 [Loo Choo and Northern Daitozima, Japan]. — Tweedie, 1950a: 92 [Aur I., Malaysia]. ?Holthuis 1953: 16. — Sakai 1956: 40 [Appendix]. — Guinot, 1958: 179, fig. 25a, b. — Serène & Luom 1958: 102 (part); 1959: 302 (part), 5G, pls IA, IIIA [Vietnam]. — Davie 2002: 523 [List].

Chlorodopsis (Cyclodius) palaoensis Sakai 1936b: 167, pls XIII, fig. 2, XIV fig. 1 [Type locality = Palau Is.]. — Miyake 1939: 215 [List].

Pilodius palaoensis Serène 1968: 80 [List].

Pilodius pilumnoides Sakai 1976: 461, text-fig. 249 a-b-b' [Ishigaki I. and Northern Daito-jima, Japan]. — Guinot 1967c: 268 [List]. — Serène 1976: 18 [Ambon I., Indonesia]; 1984, figs 143j, 150, pl. 34E [Key]. — Garth & Kim 1983: 686 [Zamboanga, Philippines]. — Takeda 1989: 166, 178 [Oshima Passage, Japan]. — Clark & Galil 1993: 1144, figs 11A–G, 36A, 42D [Singapore; Bohol and Little Santa Cruz Island, Philippines; Pulau Aur, Malaysia; Banda-Neira, Indonesia; Cape York, Bowen, Lindeman I., Lizard I., Dugong I., and Orpheus I., Australia].

Pilodius cephalalgicus Clark & Galil 1993: 1128–1129, figs 2, 17, 31(B), 40(B) [Malayan Peninsula (6°55'N, 102°45'E), Perhentian Besar, Poulo Babi Nyong (2°30'N, 103°57'E), Malaysia]. — Ng *et al*. 2008: 197 [List].

Pilodius concors Clark & Galil, 1993: 1129–1130, 1159, figs 3, 18, 32(A), 40(C) [Type Locality = Singapore; E of Hayman I., Great Barrier Reef, Cape York and Lindeman I., Australia; Poulo Condore, Vietnam; Tioman, Malaysia; Edam I., Indonesia].

Pilodius nigrocrinitus, McNeill 1968: 73 (part) [Great Barrier Reef]. (not *Pilodius nigrocrinitus* Stimpson 1859)

(?) Cancer *eurynome* Herbst 1801: 31, tab. LII, fig. 7.

(?) *Pilodius eurynome* Sakai 1999: 34, pl. 18D; Ng *et al*., 2008: 197.

(?) *Pilodius pilumnoides* Dana 1852b: 221 [Sulu Sea or Balabac Strait, Philippines]; 1855, pl. XII, fig. l0a–c.

Material Examined. *Gulf of Thailand:* 1 holotype male, 20.0 ×14.9 (MNHN B.20935), Sta. 20, 6°55'N, 102°45'E; coll. R. Serène, 24 July 1965.

Indonesia: 1 female, 14.70 × 10.00 (ZRC 2003.0559*), EA-ZJ01, Anabas, Pulau Jemaja, northern edge of Teluk Tiru, opposite Pulau Punisan, Indonesia, coll. 2 March 2002.

Malaysia: 1 male, 33.4 × 23.5 (ZRC 1965.11.11.148), Pulau Aor, South China Sea, Malaysia, coll. June 1938. — Paratype male, 58.25 × 39.20 (ZRC 1985.1506*), Tekek Bay, Pulau Tioman, Malaysia, coll. P. Ng, June 1983.

Singapore: Pilodius concors holotype male, 62.25 × 42.00 (ZRC 1965.11.11.147), Horsburgh Lighthouse, South China Sea, Singapore, coll. A.

Monteiro, April 1938. — 2 paratype males, 43.40 × 28.80 – 37.3 × 26.0, 1 paratype female (ZRC 1989.3428–3430), low tide, on rubble, Sentosa reef, Singapore, coll. P. Ng, 13 December 1989. — Paratype male, 60.70 × 42.05 (NMS 1965.11.11.149), Sultan Shoal, Singapore, coll. M Tweedie, December 1933.

Philippines: 1 male, 16.25 × 11.40 (ZRC 2013.0734*), Stn. B1, 8–14 m, 9°33.0'N 123°46.5'E, slope between reef patches, Alona Reef, Panglao Island, Philippines, coll. Panglao Expedition, 30 May 2004. — 1 female, 23.7 × 15.7 (USNM 65165), Basilan Strait, Little Santa Cruz Island, Zamboanga del Sur, Philippines, coll. T. Mortensen & F. Baker, the Mortensen Pacific Expedition, 28 February 1914. — 1 male, 9.4 × 6.6, 2 females, 9.1 × 6.4 – 10.4 × 7.7, 3 ovigerous females, 13.3 × 9.5 – 16.1 × 11.2 (ZRC 2013.1698*), Stn. B13, 3–5 m, 9°37.1'N 123°52.6'E, Baclayon Takot coral rubble, Bohol Island, coll. Panglao Marine Biodiversity Project, 15 June 2004.

Palau: 1 male, 10.75 × 7.50, 1 female, 11.10 × 7.90 (USNM 1184705), PAL 36C, 2 m, directly south of sea wall, patch reef between Urukthapel and rock island, Palau, coll. R. Kropp, 3 July 1984. — 2 females, 8.1 × 5.9 – 9.3 × 6.7 (USNM 1184748), 1 m, by large rock island toward cape, south side, Ngargol Island, Palau, coll. R. Kropp, 23 June 1984. — 1 male, 15.9 × 12.0 (UF 5119*), Stn. JAS-BEL-551, Palau, coll. J. Starmer. — 1 male, 10.15 × 7.20 (UF 3852*), GP-Loc-607, Malakal Sewer Outfall, Palau, coll. G Paulay, 26 July 1999. — 1 male, 53.30 × 35.6 (UF 2414), Stn. JAS-BEL-183, 2–5 m, Malakal, near Koror Causeway, Koror State, Palau, coll. J. Starmer, 22 July 1999.

Caroline Islands: 1 male, 14.8 × 10.0 (USNM 156080), Yap Island, Yap Islands, Caroline Islands, Micronesia, coll. R. Hiatt. — 1 female, 15.1 × 10.4 (USNM 1181389*), 7 17 34 N 134 27 13 E, 1 m, E shore of N peninsula, Urukthapel Island, Palau, coll. F. Bayer, 25 August 1955.

Vanuatu: 1 male, 17.8 × 11.6 (ZRC 2013.1653*), Site H, Vanuatu, coll. P. Clark & H. Tan, 20 September 2006.

Diagnosis. Carapace (Pl. 34B) transversely hexagonal, ca. 1.4–1.5 broad as long; surface granulate, granules larger and more conical laterally with evenly spaced short, stout, dark setae; setae usually restricted to outer margins of 1M–3M, 2L, 5L, 6L, often absent from medial regions; regions well defined by broad, deep furrows; 2M completely or incompletely divided longitudinally; 3M entire. Frontal (Pl. 34C) submedian lobes convex, margin lined with short conical granules or spines, separated by deep, U-shaped notch, lateral lobes triangular or rounded, spinose or granulate. Anterolateral margin with 4 multispinose lobes; spines curved, anteriorly directed, usually one emergent spine, several ancillary spines. Anterolateral angle of basal antennal segment expanded forming flange, completely blocking orbital hiatus. Pterygostomial region granular, with short plumose setae, often worn mesially or in large specimens. External surface of third maxilliped merus with few or no evenly space short setae, anterior margin with shallow notch. Chelipeds (Pl. 34E, F) subequal, with sparse, short and long setae, more numerous in young specimens; anterior margin of merus prominently spinose; carpus spinose or covered with conical granules, distinct furrow parallel to palmar joint; superior surface of chelae spinose or covered with conical granules, size of spines or granules decreasing inferiorly, inferior margin smooth or granulate; dark coloration of fixed finger extending proximally ca. 2/3 distance inferior surface, less than 1/2 distance external surface. Ambulatory legs (Pl. 34A) granular, moderately stout, extensor and flexor surfaces setose with many short, few long, simple setae, extensor margin spinose; dactylo-propodal locking mechanism moderately developed; tip of dactylus with long pigmented terminal spine, shorter subdistal spine. Male thoracic sternum (Pl. 34D) granulate, with short, dark setae, sometimes worn away or absent anteriorly. Male abdomen (Pl. 34D) granulate, coarsely setose, setae often worn anteriorly, medially; sutures between somites 3 to 5 slightly indicated by superficial line; somite 6 ca. longer than broad; telson longer than broad. Anterior subdistal margin of G1 (Pl. 44C) with many simple setae; tip curving posterolaterally; apical lobe long, narrow, longitudinally hollowed.

Remarks. In their revision of *Pilodius*, Clark & Galil (1993) described two species from SE Asia that are morphologically similar to *P. pilumnoides*: *P. cephalalgicus* and *P. concors*. They remarked that *P. cephalalgicus* differs from *P. pilumnoides* and *P. concors* in having chelae with pigmentation restricted to the fixed finger (versus extending proximally in *P. pilumnoides* and *P. concors*). The authors also stated that *P. concors* differs from *P. pilumnoides* and *P. cephalalgicus* in having a smooth lower external surface of the cheliped. Furthermore, Clark & Galil (1993) said that the three species could be distinguished by the G1, although they did not elaborate on this feature. However, phylogenetic analyses (Figs 14C, 15) indicated that specimens with these different features are conspecific, falling within a single well-supported clade.

Based on material examined for this study, the characters used to distinguish these species vary with age and sex. Considering other chlorodiellines, this is no surprise. Intraspecific variation in cheliped granulation has been noted in *Cyc. nitidus*, *Cyc. sculptus*, and *Cyc. ungulatus* by Gordon (1934: 32, 37) and in *Cyc. obscurus* by Forest & Guinot (1961: 109). Clark & Galil (1993) stated that pigmentation of the fixed finger cannot be used to identify females. The same is true for juveniles. A female paratype of *P. concors* (ZRC 1989.3428–3430*) has a spinose, granular lower margin of the cheliped with pigmentation restricted to the fixed finger, whereas the males in the same lot do not. Additionally, small male specimens (e.g., ZRC

2013.1698, UF 3852) morphologically congruent with *P. cephalalgicus* (i.e., granular lower external surface of the chela, pigmentation restricted to the fixed finger, and G1 morphology most similar to *P. cephalalgicus*) (Clark & Galil, 1993: 1128, figs 2, 40B), fall within the *P. pilumnoides* clade in the present analyses with a paratype of *P. concors* (ZRC 1989.3428) and a specimen identified as *P. pilumnoides* (ZRC 1965.11.11.148 = NUS 1965.11.11.148) by Clark & Galil (1993: 1145). This latter specimen has chelae with a smooth inferoexternal surface and pigmentation extending proximally of the fixed finger, but a G1 like *P. concors* (Clark & Galil 1993: fig. 11). These characters change with age. The G1s of *P. cephalalgicus*, *P. pilumnoides*, and *P. concors* (Clark & Galil, 1993: figs 2, 3, 11) display a progression in morphology corresponding with size of specimens among the three “species”. From juvenile to adult, the shaft of the G1 curves more distally and the tip elongates and closes. This progression corresponds with the size of the specimens examined by the Clark & Galil (1993) (*P. cephalalgicus*: range = 8–12 mm, mean ≈ 12.1, median ≈ 11.5; *P. pilumnoides*: range = 13–35 mm, mean = 19.2, median = 17; *P. concors*: range = 18–62, mean ≈ 35.5, median = 32). Moreover, *P. pilumnoides, P. cephalalgicus*, and *P. concors* were all described from the Malayan Peninsula, and the latter two species are narrowly distributed within the known range of *P. pilumnoides*. Based on these data, *P. concors* and *P. cephalalgicus* are synonymized with *P. pilumnoides*.

Balss (1938) synonymized *Chlorodopsis palaoensis* Sakai, 1936 with *P. pilumnoides*. Clark & Galil (1993) expressed uncertainty with the synonymy because the holotypes of *Chl. palaoensis* are female and “the black coloration on the cheliped of females is not diagnostic” (Clark & Galil 1993: 1146). This comment likely implies that Clark & Galil (1993) were uncertain whether the species is synonymous with *P. concors*, *P. cephalalgicus*, or *P. pilumnoides*.

However, this distinction does not matter, as these three species are synonyms. Sakai's (1936: pl. VIII 2) holotype is clearly a *P. pilumnoides.* Furthermore, two *P. pilumnoides* specimens from Palau (UF 5119, USNM 1181389) were recovered with *P. pilumnoides* in the present phylogenetic analyses.

Sakai (1999) provided figures of Herbst specimens, one of which is *Cancer eurynome* Herbst, 1801. In Sakai's work, Türkay commented that the species looks similar to *L. spinipes*. However, the photographed specimen appears to be *P. pilumnoides*. A re-examination of this specimen is important for securing the identity and synonymy of these species.

Clark & Galil (1993) rely of the division of the carapace region 2M for species identification. Their key to the species of *Pilodius* begins with this feature. They indicate that *P. cephalalgicus* has a 2M that is divided completely longitudinally. This feature, however, is sometimes difficult to discern, as the longitudinal furrow can be quite shallow, sometimes indiscernible posteriorly, and can be obscured by setae (e.g., ZRC 2003.0559 and USNM 1184705).

Distribution. *Pilodius pilumnoides* is restricted to the Coral Triangle and adjacent areas such as Thailand, the Caroline Islands, and Vanuatu (Pl. 51B).

Soliella gen. nov.

Key to the Species of *Soliella*

1. G1 ultimately pointing anteroventrally with apical lobe opening anteriorly (Pl. 44D). Carapace regions generally relatively deeply

defined. Supraorbital margin with relatively low spines or granules..*S. flava*

– G1 apex pointing ventrally with an apical lobe that is longitudinally hollowed with a sinuous anterior margin (Pl. 45). Carapace regions generally less deeply defined. Supraorbital margin generally with longer spines..*S. melanospinis*

Soliella flava (Rathbun, 1894)

Pls (35, 44D, 52D)

Pilodius flavus Rathbun 1894: 239 [type locality = off Sandwich Islands]; 1906: 860, fig. 21 [Kauai Channel, Laysan Island, French Frigate Shoals and Modu Manu, Hawaiian Islands]. — Edmondson 1925: 43 [Pearl and Hermes Reef and Ocean I., Hawaiian Is.]; 1933: 249 [Review]; 1962: 275, fig. 22a–b [Hawaii]. — Balss 1938a: 57 [Jaluit, Marshall Islands; Macclesfield Bank]. — Miyake 1939: 215 [Micronesia]. — Forest & Guinot 1961: 95 [Tahiti]. — Serène 1968: 80 [List]. — Peyrot-Clausade 1989: 111 [Tikehau, Tuamotu]. — DeFelice *et al*. 1998: 16 [Midway Atoll, Hawaiian Is.]. — Davie 2002: 523 [List]. — DeFelice *et al.* 2002: 30, 72 [French Frigate Shoals, Hawaiian Is.]. — Coles *et al*. 2002a: 271 [List]; 2002b: 141, 194 [Oahu, Hawaii]. — Coles *et al.* 2008: 63 [List]. — Coles & Swensen 2010: 87 [List]. — Clark & Galil 1993: 1130, figs 4A-G, 32B, 40D, 41A (part) [New Caledonia; Hawaiian Islands]. Ng *et al*. 2008: 197 [List].

Pilodius pubescens, De Man 1902: 619 [Ternate, Indonesia]. (not *Pilodius pubescens* Dana, 1852).

Pilodius melanospinis Balss 1938a: 62 (part) [?Viti Levu and Namuka, Fiji Islands].

Chlorodopsis flava Serène & Luom 1959: 330, fig. 2C, 5F, pl. IB, pi. IIIB [Review].

Chlorodopsis hawaiiensis Edmondson 1962: 273, fig. 21a-e [Oahu, Hawaii].

(?) *Pilodius pubescens*, Nobili 1907: 395 [Ohura, New Zealand (?)]. [not *Luniella pubescens* (Dana, 1852)]

(?) *Chlorodopsis melanodactylus*, Miers 1884: 531 (part) [Singapore]. (not *Pilodius melanodactylus* A. Milne-Edwards, 1873)

Material examined. *Christmas Island:* 1 male, 9.7 × 6.5 (ZRC 2013.1632*), Stn. CI-D17, S10° 25.815' E105° 40.180', reef slope, flying fish cove, Christmas Island, coll. 1 February 2010.

Philippines: 1 male, 11.65 × 7.85 (ZRC 2013.0743), Stn. B11, 2–4 m, 9°29.4'N 123°56.0'E, coral rubble, Pamilacan Island, Panglao Expedition, coll. 11 June 2004. — 2 males, 8.4 × 6.0 – 9.8 × 6.3, 2 females, 9.3 × 6.2 – 12.3 × 8.0 (ZRC 2013.0727*), Stn. B11, 2–4 m, 9°29.4'N 123°56.0'E, coral rubble, Pamilacan Island, Panglao Expedition, coll. 11 June 2004. — 1 male, 6.8 × 4.7 (ZRC 2013.1631*), Stn. B8, 3 m, °37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, Philippines, coll. Panglao Marine Biodiversity Project, 7 June 2004. — 1 male, 8.3 × 5.5, 2 juveniles (ZRC 2013.1640), Stn. B8, 3 m, °37.1'N 123°46.1'E, subtidal reef platform, Napaling, Panglao Island, Philippines, coll. Panglao Marine Biodiversity Project, 7 June 2004.

Solomon Islands: 1 male, 8.5 × 5.6 (UF 3192), Stn. ZZZ-087843, 3–5 m, under rocks and coral heads, Ghizo Island, near JFK Island, Solomon Islands, coll. H. Conley, 19 February 2002.

New Caledonia: 1 male, 10.3 × 7.0 (UF 37975*), NewC13-401, NEST16, -18.8613° 163.538°, 1–3 m, rubble, coral, sand, algae, high energy reef top, Cook Reef, New Caledonia, coll. N. Evans, 8 November 2013.

Mariana Islands: 1 male, 7.4 × 5.1 (USNM 1184650), 12 m, Pagua Patch Reef, Double Reef, Guam, coll. R. Kropp & J. Dominguez, 24 August 1984. — 1 male, 10.8 × 7.2, 2 females, 5.4 × 3.6 – 5.8 × 4.0 (USNM 1188306*), Pago Bay, Guam, coll. R. Kropp, 28 February 1984. — 1 female, 9.8 × 6.4 (UF 722), Stn. ZZZ-016534, 13.5° 144.8°, 10 m, under rubble, Pago Bay, Guam Island, Mariana Islands, USA, coll. L. Kirkendale, 30 April 1999. — 1 male, 9.7 × 6.9 (UF 26774*), Stn. GUOK10-St-022, 13.577° 144.826°, 5–16 m, Guam, Haputo, site 1, Guam Island, Mariana Islands, USA, coll. NIS team, N. Evans *et al.*, 16 June 2010.

Marshall Islands: 1 male, 10.0 × 6.8, 2 females, 8.6 × 5.8 – 12.8 × 8.3 (USNM 1181376), intertidal, Eniirikku Island, Bikini Atoll, Ralik Chain, Marshall Islands, coll. M. Johnson, 1946. — 1 male, 8.6 × 5.9 (USNM 102921), 13 m, 11 41 N 165 26 E, 1/2 mile from Aomen Island in lagoon in coral, Aomoen Island, Bikini Atoll, Ralik Chain, Marshall Islands. — 1 male, 6.5 × 4.4, 1 damaged male (USNM 266894), lagoon, Parry Island, Enewetak Atoll, Ralik Chain, Marshall Islands, coll. J. Garth, 22 July 1957. — 1 male, 10.2 × 6.9 (USNM 1181377), Bock Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. F. Bayer, 19 August 1947. — 1 male, 11.6 × 8.1 (USNM 1181373), lagoon reef, Latoback Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. F. Bayer & F. Zimmerman, 20 August 1947. — 1 male, 12.4 × 8.4, 1 ovigerous female, 9.8 × 6.5 (USNM 1181384), lagoon reef, Latoback Island, Rongerik Atoll, Ralik Chain, Marshall Islands, coll. F. Bayer & F. Zimmerman, 21 August 1947.

Micronesia: 1 male, 10.5 × 7.0, (USNM 106531), halfway between Elangalap and northwest tip of Falarik Islet, Ifalik Atoll, Yap, Micronesia, Caroline Islands, Fourth Pacific Atoll Survey, coll. 21 September 1953.

Kiribati: 1 male, 13.1 × 8.6 (USNM 93998), 2–5 m, 3.25 miles N 31 degrees from Tabuarorae Maneaba near center of Te Rawa Ni Bao, Onotoa Atoll, Gilbert Islands, Kiribati, coll. P. Cloud, 23 August 1951. — 1 female, 8.1 × 5.5, 2 ovigerous females, 12.0 × 8.2 – 13.0 × 9.1, 1 juvenile (UF 10524*), Stn. GP-Loc-827-DP, 1.9841° -157.4819°, 10–12 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, just N of main reef passage, W side of atoll, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay & N. Knowlton, 5 August 2005. — 1 juvenile (UF 11005*), Stn. GP-Loc-826-DP, 1.9923° -157.4841°, 10–14 m, dead *Pocillopora verrucosa*? head, outer reef slope, N of main reef passage, W side of atoll, Kiritimati Atoll, Line Islands, Kiribati, coll. N. Knowlton & G. Paulay, 5 August 2005. — 1 male, 10.4 × 7.1 (UF 10515*), Stn. GP-Loc-824-DP, 2.0086° -157.4895°, 10–14 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, W side of Atoll, N of Passage, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay & N. Knowlton, 4 August 2005. — 1 male, 11.3 × 7.4 (UF 10521*), Stn. GP-Loc-836-DP, 1.8563° -157.5539°, 10–20 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, ca. 1 mile E of SW Point, Along S side of Atoll, Kiritimati Atoll, Line Islands, Kiribati, coll. G. Paulay & N. Knowlton, 9 August 2005.

Hawaiian Islands: 1 holotype female, 9.0 × 6.2 (USNM17317), Kaiwi Channel, Hawaiian Islands, coll. Albatross. — 1 male, 11.72 x 8.49, 1 ovigerous female (AMNH 9620), Midway Island, Pacific Ocean, coll. Phil Spicer, From W. J. Clench, February–March 1941. — 1 male, 12.75 x 8.46 (USNM 29538) (this one has a hawaiiensis G1), Stn. 4148, U.S. Fish Commission, Steamer Albatross, Modu Manu Island, Hawaiian Islands, det. Rathbun. — 1 male (UF 12254*), Stn. FFS-0168, 23.7683° -166.2602°, 31 m, under rocks, basalt pinnacle in lagoon, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 23 October 2006. — 1 male, 8.8 × 5.8 (f/UF 12342), Stn. FFS-0091, 23.8733° -166.2347°, 15 m, back reef, French Frigate Shoals, Hawaiian Islands, USA, coll. R. Brainard & B. Zgliczynski, 16 October 2006. — 1 male, 13.3 x 8.8 (USNM 30587), 20-30 fms., sta. 3954, U.S. Fish Commission, Steamer Albatross, Vic Laysan Island, Hawaiian Islands, coll. 1902, det. M. Rathbun. — 1 male, 15.7 × 10.4 (UF 12254), BFFS-947, FFS-0168, 31 ft, 23.7683° -166.2602°, hand collected, under rocks, basalt pinnacle in lagoon, French Frigate Shoals, coll. G. Paulay *et al*., 23 October 2006. — 1 male, 11.7 × 8.5, 1 ovigerous female, 11.0 × 7.9 (AMNH 11606), Midway Island, coll. P. Spicer, February-March 1941. — 1 male, 10.0 × 6.7, 1 female, 9.0 × 5.9 (ZRC 2013.1641), Stn. FFS-6, French Frigate Shoals, coll. 11 September 2000. — 1 female, 11.3 × 7.6 (UF 12140*), Stn. FFS-0087, 23.8732° -166.2348°, 4 m, under rocks, reef crest, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 16 October 2006. — 1 male, 9.8 × 6.6, 1 female, 8.6 × 5.6 (UF 12223*), Stn. FFS-0142, 23.7695° -166.2608°, 32 m, under rocks, basalt pinnacle in lagoon, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 21 October 2006. — 1 male, 10.8 × 7.7, 1 female, 9.1 × 6.6 (UF 12079*), Stn. FFS-0046, 23.6577° -166.0738°, 80 m, fore reef, French Frigate Shoals, Hawaiian Islands, USA, coll. R. Brainard & B. Zgliczynski, 13 October 2006. — 1 male, 10.3 × 7.4 (UF 12153*), Stn. FFS-0087, 23.8732° -166.2348°, 4 m, under rocks, reef crest, French Frigate Shoals, Hawaiian Islands, USA, coll. G. Paulay *et al.*, 16 October 2006.

Society Islands: 1 male, 11.9 × 8.0 (UF 15458*), Stn. MIB_009, -17.4758° -149.8314°, from within rubble, outer reef slope, mid N coast, off Sheraton Hotel, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al.*, 12 October 2008. — 1 male, 12.1 × 8.0 (UF 16161*), Stn.

MIB_065, -17.47747° -149.84116°, 1–2 m, brushed from under rubble, mid-barrier reef, W of Cook's Bay Pass, lagoon reef, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al.*, 18 October 2008. — 1 male, 8.7 × 5.7 (UF 15457*), Stn. MIB_009, -17.4758° -149.8314°, from within rubble, outer reef slope, mid N coast, off Sheraton Hotel, Moorea Island, Society Islands, French Polynesia, coll. S. McKeon *et al.*, 12 October 2008.

Tuamotu Islands: 1 male, 13.0 × 8.4 (UF 35352), Stn. GAVA-23, -21.334° -136.6328°, 33.68 m, windward fore reef, Vahanga Atoll, Tuamotu Archipelago, French Polynesia, coll. J. Moore, 24 January 2013. — 1 male, 12.2 × 7.9 (UF 18458), Stn. Bacchet-001, reef flat, Mekemo, Makemo Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, April 2009. — 2 males, 10.3 × 6.5 – 13.2 × 8.5 (UF 18484), Stn. Bacchet-001, reef flat, Mekemo, Makemo Atoll, Tuamotu Islands, French Polynesia, coll. P. Bacchet & J. Letourneaux, April 2009.

Diagnosis. Carapace (Pl. 35B) transversely hexagonal, ca. 1.5 broad as long; surface covered in short, stout light-colored setae, few long, light-colored setae regions well defined, separated by wide, relatively deep, smooth furrows; 2M entire or feebly divided anteriorly, 3M entire. Submedian lobes of front (Pl. 35C) convex, margin lined with granules, separated V- or U-shaped notch; lateral lobes triangular, granulate. Outer margin of orbits with short spines on dorsal side. Anterolateral margin with four spinose lobes. Anterolateral angle of basal antennal segment slightly expanded, entering less than halfway into orbital hiatus. Pterygostomial region minutely granulate, with plumose setae diagonally from posterior to lateral surface. Chelipeds (Pl. 35E, F) subequal, covered with long, simple, light-colored setae, spinose; merus stout. Ambulatory legs (Pl. 35A) stout, setose; setae long, simple, light-colored; extensor margin of merus lined with long spines; tip of dactylus with long pigmented spine, short subdistal spines. Male thoracic sternum (Pl. 35D) minutely granulate, with few long scattered setae. Male abdomen (Pl. 35D) moderately stout, few long posterior setae; somite 6 ca. broad as long; telson ca. broad as long. G1 (Pl. 44D) slender, distal 1/4 curved ventrally; apex pointing anteroventrally with stout subdistal setae; apical lobe almost tubular, opening facing anteriorly.

Remarks. *Soliella flava* and *S. melanospinis* are difficult to differentiate based on external morphology. Rathbun described both species. In her description of *S. melanospinis*, Rathbun (1911) stated that *S. flava* has a less deeply areolated carapace, a dorsum devoid of spines, and an upper margin of the orbit without spines (vs. less deeply areolated regions and a spinose dorsum and upper margin of the orbit in *P. melanospinis*). Serène (1984) stated that the spination on the upper margin of the orbit was a good character for differentiation, but that the difference in the areolation of the carapace was difficult to assess. He also stated that the G1s are similar, although he had provided figures of the two in his previous publication with Nguyen (Serène & Nguyen, 1959: fig. 2C, M). Then Edmondson (1962) described *Chlorodopsis hawaiiensis* without comparison with *S. flava* or *S. melanospinis*. He also provided illustrations of their G1s.

After examining specimens of each species, Clark & Galil (1993) synonymized *S. melanospinis* and *S. hawaiiensis* with *S. flava*. However, there were two distinct, divergent clades recovered in the present molecular analyses, and there are three different G1 morphotypes in the literature. In his publication on Hawaiian xanthids, Edmondson (1962: figs 21d, 22b) provided figures of the ladle-like G1 of *Chlorodopsis hawaiiensis* and the tubular G1 of *S. flava*. Edmondson's figures are clearly different, but simplistic. Furthermore, Rathbun's (1907) Hawaiian holotype of *S. flava* is female, which complicates matters. After examination of many Hawaiian specimens, it seems clear that the *Chlorodopsis hawaiiensis* and *S. flava* G1s represent slight variation that is exaggerated in Edmondson's (1962) figures. These gonopod morphotypes fall within the *S. flava* clade in the present analysis. The third G1 morphotype was illustrated by Clark & Galil (1993: fig. 4D–G) as *S. flava*, although their specimen is a paratype of *S. melanospinis*. This is the same morphotype as those illustrated by Serène & Nguyen (1959: fig 2M) and Serène (1984: fig. 146), but correctly identified as *S. melanospinis*.

In summary, Rathbun's (1911) external morphological characters are difficult to appreciate, but there are clearly two species. Although the depth of the furrows separating the carapace regions and spination of the supra orbital margin vary, *S. flava* specimens do generally have deeper defined carapace regions and a less spinose supraorbital margin (versus less defined regions and spinose orbital margin in *S. melanospinis*). However, these characters display too much variation, especially in small individuals, to be used without caution. The G1 morphology is the only reliable character for identification. *Soliella flava* has a G1 pointing anteroventrally with an apical lobe opening anteriorly (Pl. 44D) [versus apex pointing ventrally with an apical lobe that is longitudinally hollowed with a sinuous anterior margin (Pl. 45)].

Distribution. *Soliella flava* is reported from Hawaiian and French Polynesia to the Coral Triangle and Christmas Island (Pl. 52D).

Soliella melanospinis (Rathbun, 1911)

Pls (36, 45, 53A)

Chlorodopsis melanospinis Rathbun 1911: 226, pl. 18, fig. 11 [Saya de Malha, Amirante]. — Balss 1938a: 62 (part) [Tamatave, Madagascar]; Serène & Luom 1958: 108, pl. I, fig. D, pl. III, fig. b, pl. IV, fig. C [Vietnam]; 1959: fig. 2M [Vietnam].

Pilodius melanospinis Guinot 1964b: 67 [Aldabra]; 1967c: 268 [List]. — Serène 1968: 80 [List]; 1984: 242, figs 143e, 146, pl. XXXIIIE [Ile Maurice; Ile Aldabra]. — Serène *et al*. 1976: 18 [Ambon I., Indonesia]. — Dai *et al.* 1986: 306, pl. 43(4), fig. 166(1) [Review]. — Dai & Yang 1991: 329, pl. 43(4), fig. 166(1) [Review].

(?) *Chlorodopsis pilumnoides*, Laurie 1906: 406. [Gulf of Manaar, Jokkenpiddi Paar, and Muttuvaratu Paar, Sri Lanka]. [not *Pilodius pilumnoides* (White, 1848)]

Material examined. *Comoros Islands:* 1 female, 10.5 × 7.0 (UF 13702), Stn. MAY08-St5, -12.859323° 45.268639°, 0–3 m, reef flat, Passe en S, Mayotte Island, Comoros Islands, France, coll. A. Anker & F. Michonneau, 2 June 2008.

Scattered Islands: 1 male, 12.1 × 8.0 (UF 20665*), Stn. JDNO-11, -17.01445° 42.80278333°, 10–20 m, Iles Eparses, Juan de Nova, NE of island, offshore shoal, Juan de Nova Island, Scattered Islands, France, coll. 28 April 2009. — 1 male (damaged), 1 juvenile (UF 21189), Stn. GLOR-2, -11.59088333° 47.28513333°, 7–14 m, reef platform and shallow canyons, Iles Eparses, Glorieuses, Glorieuses Island, Scattered Islands, France, coll. H. Bruggemann *et al.*, 4 May 2009. — 1 male, 6.3 × 4.3 (UF 21139), Stn. GLOR-2, -11.59088333° 47.28513333°, 7–14 m, reef platform and shallow canyons, Iles Eparses, Glorieuses, Glorieuses Island, Scattered Islands, France, coll. H. Bruggemann, M. Malay *et al.*, 4 May 2009.

Reunion Island: 1 male, 8.6 × 5.9 (UF 12760), Stn. SWIO-16, -21.19358333° 55.28243333°, 8–16 m, under rocks, fore reef, Saint-Leu, Maison Verte/Cimetière, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann, *et al.*, 13 August 2007. — 1 male, 8.4 × 5.6 (UF 12911*), Stn. SWIO-26, -21.153333° 55.28111666°, 6–15 m, extracted from rubble, rocky slope / basalt blocks / fore reef, Saint-Leu, Sec Jaune, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al.*, 17 August 2007. — 1 male, 10.1 × 6.5 (UF 12825*), Stn. SWIO-4, -21.02015833° 55.23211111°, 10–15 m, in coral matrix (mostly from dead *Pocillopora*), fore reef, Boucan Canot, Paine au Sucre, Reunion Island, Mascarene Islands, France, coll. H. Bruggemann *et al.*, 6 August 2007.

Sri Lanka: 1 male, 12.1 × 8.8 (ZRC 1970.1.20.2), Colombo Museum, Colombo, coll. 1966.

Seychelles: 1 male, 10.7 x 7.3 (USNM 41269), 53 m, Amirante Islands, Seychelles, coll. J. Gardiner, Sealark Expedition, Sealark H.M.S., 9 October 1905.

Saya del Malha: 1 holotype male, 17.0 × 11.4, 3 females, 5.5 × 3.9 – 12.0 × 8.2 (USNM 41268), 53 m, W. Indian Ocean, Saya del Malha Bank, coll. Sealark Expedition, Sealark R/V, 7 September 1905.

Chagos: 1 male, 13.00 × 8.90, 2 females 6.6 × 4.5 – 6.9 × 4.8, 1 ovigerous female, 9.2 × 6.5 (ZRC 2013.0782*), CH0565, 10m approx., dead branching coral heads, outer reef, Peros Banhos Chagos Archipelago, coll. C. Head & H. Koldeway, 25 February 2013. — 1 male, 7.0 × 4.7 (ZRC 2013.0777*), CH0833, 10m approx., dead branching coral heads, outer reef, Diego Garcia Chagos Archipelago, coll. C. Head & H. Koldeway, 3 March 2013. — 1 male, 15.10 × 10.00, 3 females, 6.4 × 4.3 – 14.0 × 9.2, 1 juvenile (ZRC 2013.0774), CH0793, 10m approx., dead branching coral heads, outer reef, Egmont, Chagos Archipelago, coll. C. Head & H. Koldeway, 1 March 2013. — 1 male, 12.35 × 9.65, 1 ovigerous female (CH–0638). — 1 male, 11.65 × 7.85 (ZRC 2013.0770) CH0220, 10m approx., dead branching coral heads, outer reef, Salomon, Chagos Archipelago, coll. C. Head, & H. Koldeway, 19 February 2013.

Australia: 1 male, 8.5 × 6.10 (UF 25780*), AUST-6331, HI09-104, -23.4284° 151.9546°, Heron Island, Queensland, Australia, coll. J. Reimer, 25 November 2009. — 1 male, 18.1 × 12.1 (UF 21947), Stn. NIN09-St-36, -22.58104° 113.7618°, 10 m, in *Pocillopora* head #6, reef slope, Ningaloo Reef, outside of North Channel entrance, Western Australia, Australia, coll. J. Caley & L. Plaisance, May 2009. — 1 male, 16.5 × 11.4 (UF 21526), Stn. NIN09-St-12, -22.72603° 113.6138°, 0–20 m, patches of live corals and rubble on sand, Ningaloo Reef, outside reef, Western Australia, Australia, coll. 15 May 2009. — 1 male, 12.7 × 8.6 (UF 22414*), Stn. NIN09-St-70, -22.60826° 113.6249°, 10 m, in *Pocillopora* head #11, reef front, Ningaloo Reef, Wreck Zirv, Western Australia, Australia, coll. J. Caley & L. Plaisance, May 2009. — 1 male, 8.9 × 6.0 (UF 24812*), Stn. HI09-011, -23.47221667° 151.9504667°, 9–10 m, in rubble, reef slope, coral cover, rubble patches, Heron Island, Pinacle, Queensland, Australia, coll. S. McKeon, 13 November 2009. — 1 male, 12.3 × 8.8 (UF 17379), Stn. AUST-ST-077, 25–30 m, deep rubble, *Pocillopora* heads, fore reef, Lizard Island, Day Reef, station 2, Queensland, Australia, coll. S. Smith & K. Mills, 22 February 2009. — 1 male, 11.2 × 7.7 (UF 18462), Stn. AUST-ST-042, 2–3 m, rubble, back reef flat, coral, rubble, sand, Waining Reef, 2nd snorkelling site, Queensland, Australia, coll. C. Watson, 15 February 2009.

Taiwan: 1 female, 11.8 × 8.2 (UF 11892*), Stn. MTAI-03, 21.95521° 120.77003°, 10–20 m, under coral, fringing reef, Tiaoshi, SE of Nanwan Bay, Kenting County, Taiwan, coll. M. Malay, 28 June 2007.

Japan: 1 male, 13.6 × 9.1 (UF 26958*), Stn. GUOK10-St-062, 24.42585° 123.765883°, 4 m, under rock, fore reef, Iriomote, Unari-Zake, Iriomote Island, Okinawa Prefecture, Japan, coll. N. Evans *et al.*, 8 July 2010. — 1 female, 11.2 × 7.7 (UF 7177*), Stn. GP-Loc-799, 26.7391667°

127.81008333°, 18–22 m, under rocks, outer reef slope, Ie Island, Kananzaki: NW end of Island, Okinawa, Japan, coll. G. Paulay & Kinjo, 8 July 2004.

Caroline Islands: 1 female, 11.1 × 7.6 (UF 3896*), Stn. BPAL-085, 7.262333° 134.5481667°, 10–15 m, under rocks, outer reef slope, Uchelbeluu Reef, Palau, coll. G. Paulay, 4 March 2003. — 1 ovigerous female, 14.8 × 10.0 (UF 3902*), Stn. BPAL-103, 7.2561667° 134.4528333°, 5–15 m, under rocks, fore reef, off Middle of Steep Eastern Slope of Ngeremdiu Mt., Palau, coll. G. Paulay, 7 March 2003.

Papua New Guinea: 1 female, 9.7 × 6.6 (UF 3497), Stn. GP-Loc-565, 36 m, Louisiade Archipelago, off Tagula, about 200 meters from Mangrove Fringed Shore, Milne Bay Province, Papua New Guinea, coll. G. Paulay, 3 June 1998.

Solomon Islands: 1 male, 11.2 × 7.7 (UF 3362*), Stn. ZZZ-087897, 3–6 m, under rocks and coral, on reef, Near Ghizo City, Ghizo Island, Solomon Islands, coll. H. Conley, 20 February 2002. — 1 male, 14.0 × 9.7 (UF 2544*), Stn. ZZZ-087065, 3–20 m, among rocks and coral, Near JFK Island, Ghizo Island, Solomon Islands, coll. H. Conley, 13 February 2002.

Vanuatu: 1 male, 9.2 × 6.3 (ZRC 2013.1636), Stn. DB75, 20 m, 15°22.9'S, 167°11.9'E, sand and dead corals, SE Matewulu, Vanuatu, coll. Santo Marine Biodiversity Survey, 28 September 2006. — 1 male, 9.3 × 6.4, 2 females, 6.5 × 4.4 – 6.8 × 4.8, 1 ovigerous female, 10.8 × 7.3 (ZRC 2013.1633), Stn. DB63, 21 m, 15°26.9'S, 167°15.8'E, sand, dead and live corals, SE Aésé Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 25 September 2006. — 1 male, 11.5 × 7.9 (ZRC 2013.1634*), Stn. DB67, 7 m, 15°22.9'S, 167°13.1'E, sand and dead corals, W Mavéa Island, Vanuatu, coll. Santo Marine Biodiversity Survey, 26 September 2006. — 1 female, 9.7 × 6.3 (ZRC 2013.1635), Vanuatu, coll. Santo Marine Biodiversity Survey, October 2006.

Diagnosis. Carapace (Pl. 36B) transversely hexagonal, ca. 1.5 broad as long; surface covered with short, stout light-colored setae, and few long, light-colored setae; regions well defined, separated by wide, smooth furrows; 2M entire or feebly divided anteriorly, 3M entire. Submedian lobes of front (Pl. 36C) convex, margin lined with granules, separated V- or U-shaped notch; lateral lobes triangular, spinose. Outer margin of orbits with long spines on dorsal side. Anterolateral margin with four spinose lobes. Anterolateral angle of basal antennal segment slightly expanded, entering less than halfway into orbital hiatus. Pterygostomial region minutely granulate, with plumose setae diagonally from posterior to lateral surface. Chelipeds (Pl. 36E, F) subequal, covered with long, simple, light-colored setae, spinose; merus stout. Ambulatory legs (Pl. 36A) stout, setose; setae long, simple, light-colored; extensor margin of merus lined with long spines; tip of dactylus with long pigmented spine, short subdistal spines. Male thoracic sternum (Pl. 36D) minutely granulate, with few long scattered setae. Male abdomen (Pl. 36D) moderately stout, few long posterior setae; somite 6 ca. broad as long; telson ca. as broad as long. G1 (Pl. 45) slender, distal 1/4 curved ventrally; apex pointing ventrally with stout subdistal setae; apical lobe almost spatulate, longitudinally hollowed with sinuous anterior margin.

Remarks. See Remarks for *Soliella flava*.

Distribution. *Soliella melanospinis* occurs from the Western Indian Ocean to the Western Pacific. It is present in the Coral Triangle and nearby in Taiwan, Japan, Palau, the Solomon Islands, and Vanuatu (53A).

Conclusion

The combination of historical taxonomic literature, G1 and other morphology, genetree analysis, and cluster analysis aided in delineation and shed light on the evolutionary history of the Chlorodiellinae, despite conflicts in the data. By and large, the sole use of G1 morphology indicated mistakes in taxonomic literature—e.g., synonymy of *Pilodius concors*, *P. cephalalgicus*, and *P. philippinesis*. COXI genetrees supported species delimited based on G1 morphology. Each morphological species was recovered as a well-supported monophyletic clade, with only two exceptions: *Cyclodius sculptus* and *Chlorodiella nigra*. However, given the prevalence of paraphyletic species (roughly 20%) outlined by Funk & Omland (2003) and Ross (2014), low levels of paraphyletic species is expected. One potential source of discrepancy between COXI data and morphology was the presence of subclades within morphotypes. However, each of these clades had a distinct geographic distribution with relatively limited overlap in distribution. This combined with the relatively recent splits of these subclades likely indicates incipient speciation.

Differences in G1 morphology likely indicates reproductive isolation. All of the presently defined species have distinct G1 morphologies. The HSC and BSC are therefore in agreement with the species present in the systematic account. According to the PSC (*sensu* Mishler and Theriot) the species delineated here may or may not be the "least inclusive taxon recognized in a formal phylogenetic classification." The subclades within G1 morphotypes are monophyletic and seem to have a "biological process" that has allowed the clades to differentiate in COXI. However, a different choice in genes—one with a slower rate of evolution—may produce a different result.

Therefore, basing species assignment on COXI would be arbitrary. To use the language of Mishler and Theriot (2000), these subclades do not seem “worthy of formal recognition” as species given their restricted ranges, recent divergence, and lack of morphological differentiation. Wheeler & Platnick’s (2000) PSC states that species are the “smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states”. The present delineation based on morphology and monophyly satisfies this concept. The same is true of the ESC. Based on G1 morphology and monophyly, the presently delineated chlorodielline species are reproductively isolated, and reproductive isolation between populations satisfies the ESC criteria that species have different “evolutionary fates” and “historical tendencies”.

List of Species

CHLORODIELLINAE NG & HOLTHUIS , 2007

Chlorodiella barbata (Borradaile, 1900)

Chlorodiella cochlearis (Zehntner 1894)

Chlorodiella cytherea (Dana, 1852)

Chlorodiella planapexa sp. nov.

Chlorodiella laevissima (Dana, 1852)

Chlorodiella martensi (Krauss, 1843)

Chlorodiella nigra (Forskål, 1775)

Chlorodiella ohshimai (Miyake & Takeda, 1976)

Chlorodiella quadrilobata Dai, Cai & Yang, 1996

Chlorodiella xishaensis Chen & Lan, 1978

Cyclodius drachi (Guinot, 1964)

Cyclodius granulatus (Targioni-Tozzetti, 1877)

Cyclodius granulosus De Man, 1888

Cyclodius nitidus (Dana, 1852)

Cyclodius obscurus (Hombron & Jacquinot, 1846)

Cyclodius paumotensis (Rathbun, 1907)

Cyclodius ungulatus (H. Milne Edwards, 1834)

Luniella pubescens (Dana, 1852)

Luniella pugil (Dana, 1852)

Luniella scabricula (Dana, 1852)

Luniella spinipes (Heller, 1861)

Pilodius areolatus (H. Milne Edwards, 1834)

Pilodius granulatus Stimpson, 1859

Pilodius maotieni Serène, 1971

Pilodius miersi (Ward, 1936)

Pilodius moranti Clark & Galil, 1993

Pilodius nigrocrinitus Stimpson, 1859

Pilodius pilumnoides (White, 1848)

Soliella flava (Rathbun, 1894)

Soliella melanospinis (Rathbun, 1911)

CHAPTER 6.

GENERAL DISCUSSION AND CONCLUSION

The subfamily Chlorodiellinae is now delimited and revised using molecular phylogenetics and morphology. Two new chlorodielline genera are described and the several genera, including *Ratha* Lasley *et al*. 2013, have been removed. Each species is delimited and treated with accompanying diagnoses, figures, and keys. One new species is described. Delineation was possible with the aid of integrated morphological, geographic, and molecular data. Reproductive isolation was used as a criterion for delineation and several major species concepts were discussed. The chlorodielline phylogeny has shed light on the taxon's placement in Xanthidae, on generic relationships, and species delineation.

The presented stable taxonomy and well-supported phylogeny of Chlorodiellinae lends the group for use as a model for exploring marine speciation. Based on preliminary data, the subfamily appeared to be a good model for a biogeographic reconstruction that could be used to infer ancestral range and test whether the coral triangle is a center of origin (e.g., Cabezas *et al*. 2012). The basis for this idea was the prior understanding of species distributions and an early phylogeny. Several of the most recently split species pairs in Chlorodiellinae (*Cyclodius granulatus* and *Cyc. nitidus*, *Pilodius maotieni* and *P. nigrocrinitus*, *P. miersi* and *P. granulatus*, and *Chlorodiella nigra* and *Chl. xishaensis*) appeared to have an interesting pattern: one species restricted to the Coral Triangle and adjacent areas, and the other more widespread. This pattern seemed to indicate that speciation occurs within or near the Coral Triangle in the Chlorodiellinae. The same pattern was found in COXI data in many species—i.e., basal or sister taxa are often restricted to the coral triangle (pers. obs). However, the examination of thousands of specimens during the progress of the present study revealed that these restricted ranges were just an artifact of insufficient geographic sampling. Based on the present study, the coral triangle has the highest diversity in the Indo West-Pacific of chlorodielline crabs than any other region, but most of the species thought to be endemic to the area have wider distributions. These data made testing the coral triangle as a center of origin impractical, especially in light of the known difficulties with performing these analyses with marine organisms—e.g., larval dispersal, plate tectonics, a priori definition of species areas, and concealed extinction (Barber & Bellwood, 2005).

Despite this complication, some interesting patterns have emerged that could provide insight into the evolutionary history of the taxon. For instance, all *Pilodius* species except *P. areolatus* have similarly restricted ranges relative to most of the other chlorodielline species, which generally have more widespread Indo-West Pacific ranges. Larval duration is correlated with species range or habitat preference (Paulay & Meier 2006). Xanthids generally have four zoeal stages (Wear 1970, Rice 1980). Gohar & Al-Kholy (1957) confirmed that *Chl. nigra* is a typical xanthid in illustrating the species' four zoeal stages. Furthermore, the first zoeal stages of *Cyc. obscurus*, *Cyc. paumotensis*, *P. areolatus*, and *L. pugil* have been studied (Ng & Clark, 2000; Clark & Paula, 2003). From what is known of the first zoeal stages of these species, they likely have four stages (P. Clark, pers. comm.). However, Terada (1982) showed that *P. nigrocrinitus* is atypical in having only three larval stages. This is interesting, as the species has a relatively narrow distribution, occurring in the Coral Triangle and adjacent areas. It would be interesting to investigate whether other *Pilodius* species also have three stages, as the one known species of *Pilodius* has an uncommonly reduced three stages. Reduction of larval stages has been documented in estuarine crab species, and the number of larval stages is usually conserved in genera (Rice 1980).

Another possible evolutionary pattern involves the relationship between the degree of interspecific difference in G1 morphology and geographic range overlap. The relationship between range overlap, G1 differentiation and phylogeny is especially evident in the *Chl. laevissima* and *Chl. cytherea* groups. The five *Chl. cytherea* clades are unusual in having relatively narrow allopatric or parapatric distributions (versus generally widespread and/or overlapping in chlorodielline species) and indistinguishable and variable G1s (versus generally distinct, invariable G1s chlorodielline species). These idiosyncrasies are especially interesting when compared to the groups' closest relative, the *Chl. laevissima* complex. This latter complex comprises three species (*Chl. laevissima*, *Chl. martensi*, and *Chl. planapexa* sp. nov.) that contrast with *Chl. cytherea's* clades in distribution and G1 morphology. That is, *Chl. laevissima* complex species have widespread, overlapping ranges and distinct G1s. These complexes have relatively recently radiated. Based on these data and corroboration of other chlorodielline sister-species pairs, the subfamily may be a good model for testing reinforcement of allopatric speciation via reproductive character displacement (e.g., Hollander *et al*. 2013, Sauer & Hausdorf 2009).

The present thesis advances a stable framework for chlorodielline classification while advocating future systematic work on this most diverse family of crabs. Data presented are useful for understanding evolutionary mechanisms, ecology, conservation and biodiversity in this group with implications on speciation in the sea. Further integration of molecular and traditional systematics will continue to shed light on the complicated taxonomy of the xanthidae—an ambitious but important goal. Our understanding of their evolutionary relationships has steadily increased since MacLeay's (1838) description of the subfamily, but there are many unresolved questions. This, despite these crabs being among the most abundant, ubiquitous, ecologically important reef and rocky-shore associates. A solid taxonomic framework of these crabs will inform biodiversity, conservation, ecology, and evolution in the sea.

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PHOTOGRAPHIC PLATES

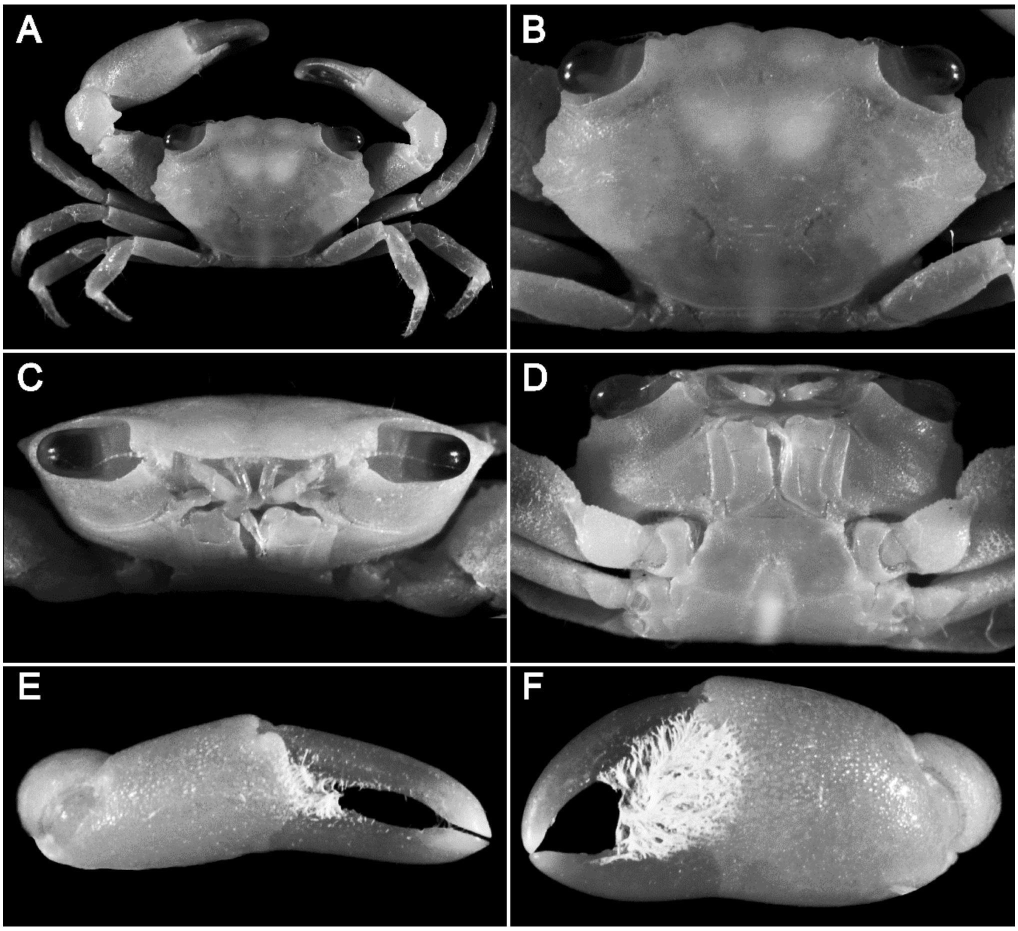


Plate 1. *Chlorodiella barbata* (Borradaile, 1900), male, 6.2 × 4.1 (USNM 33258), Tuvalu; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

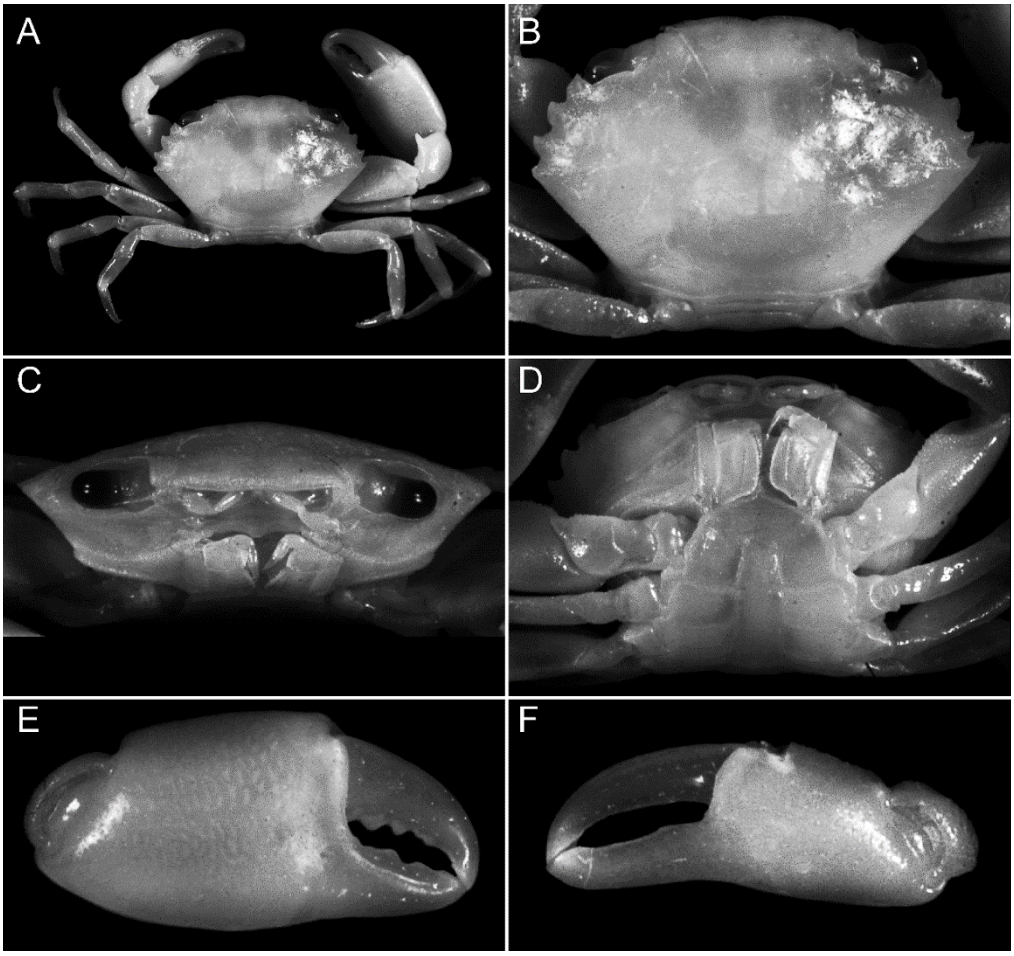


Plate 2. *Chlorodiella cochlearis* (Zehntner 1894), male, 7.5 × 5.0 (ZRC 2013.0453), Philippines; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

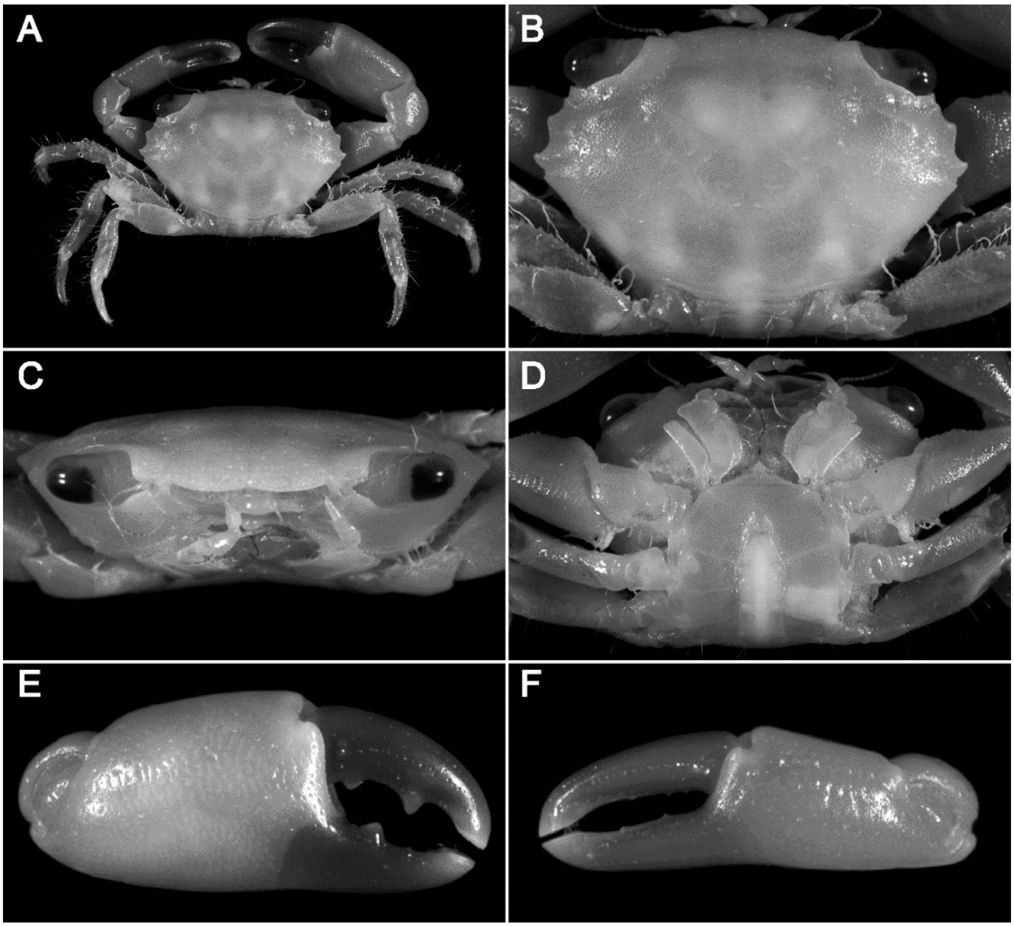


Plate 3. *Chlorodiella cytherea* (Dana, 1852) form 1, male, 8.1 × 5.1 (UF 12341), Hawaiian Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

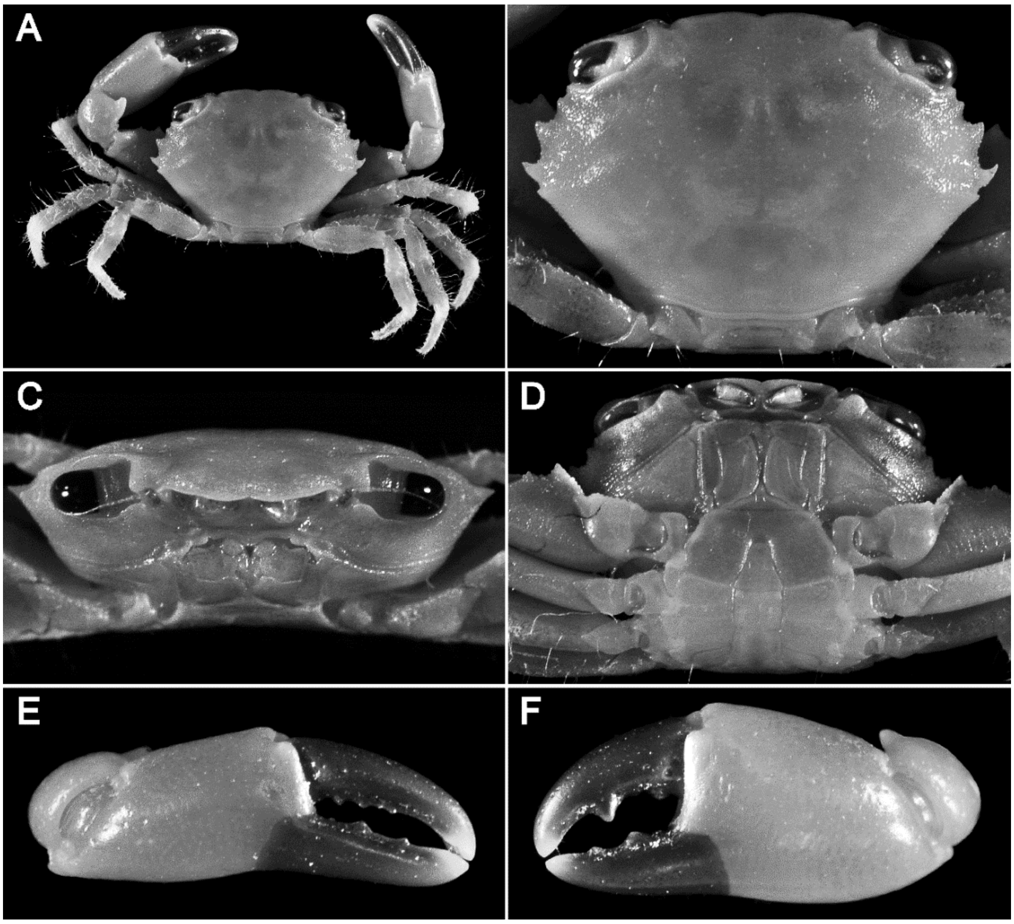


Plate 4. *Chlorodiella cytherea* (Dana, 1852) form 5, 7.5 × 5.0 (UF 36830), Red Sea; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

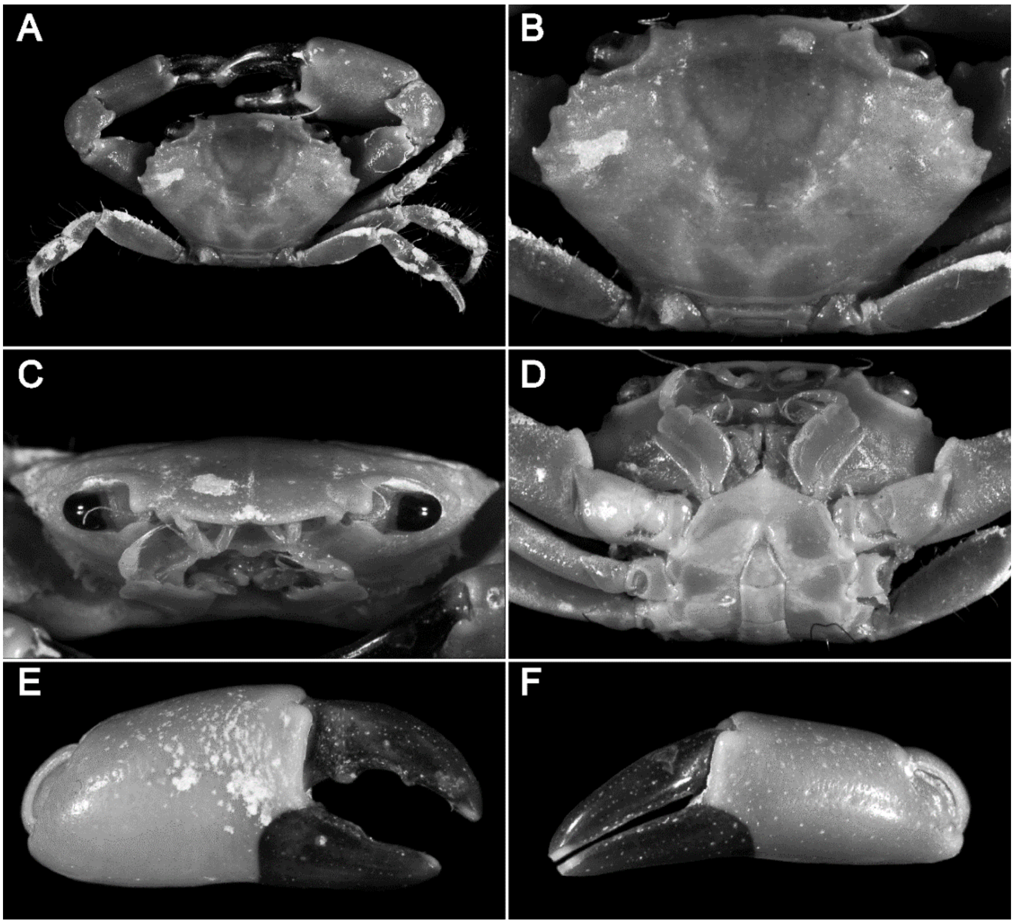


Plate 5. *Chlorodiella cytherea* (Dana, 1852) form 2, male, 11.5 × 7.4 (UF 2912), Guam; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

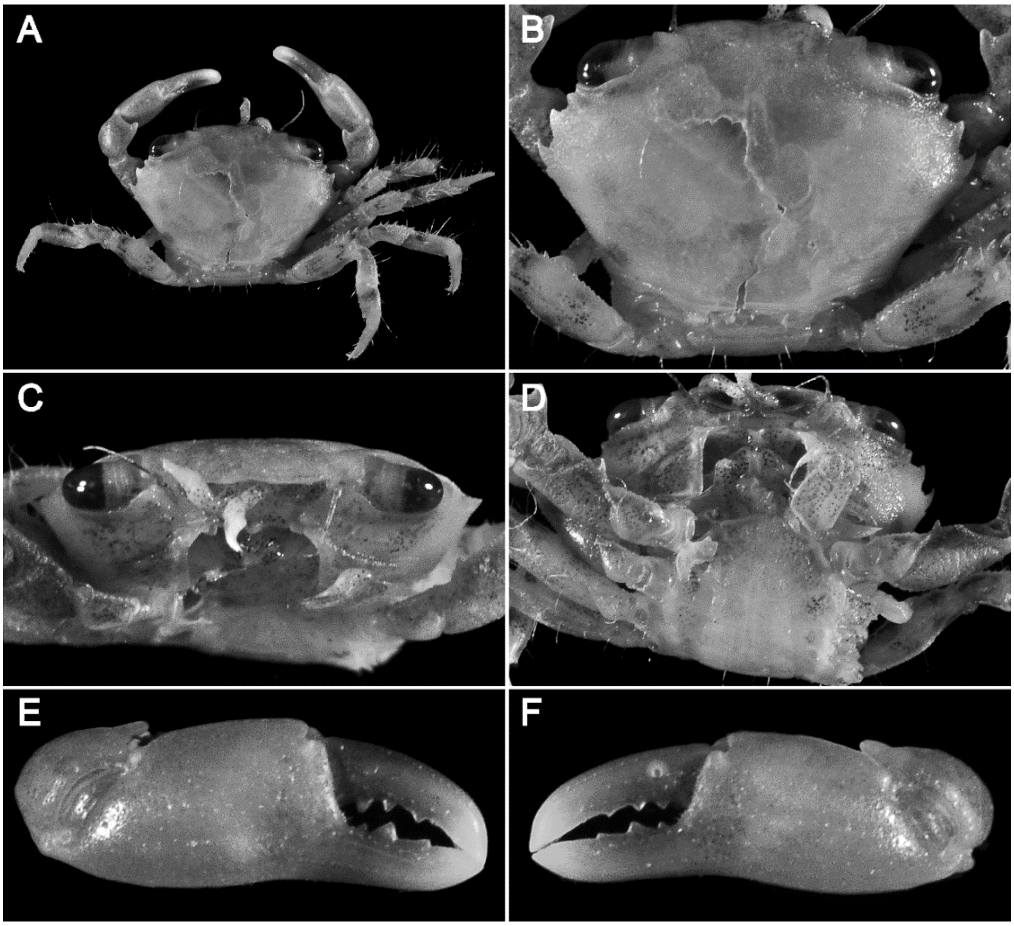


Plate 6. *Chlorodiella cytherea* (Dana, 1852) form 3, 5.8 × 3.9 (ZRC 2013.1699), Indonesia; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

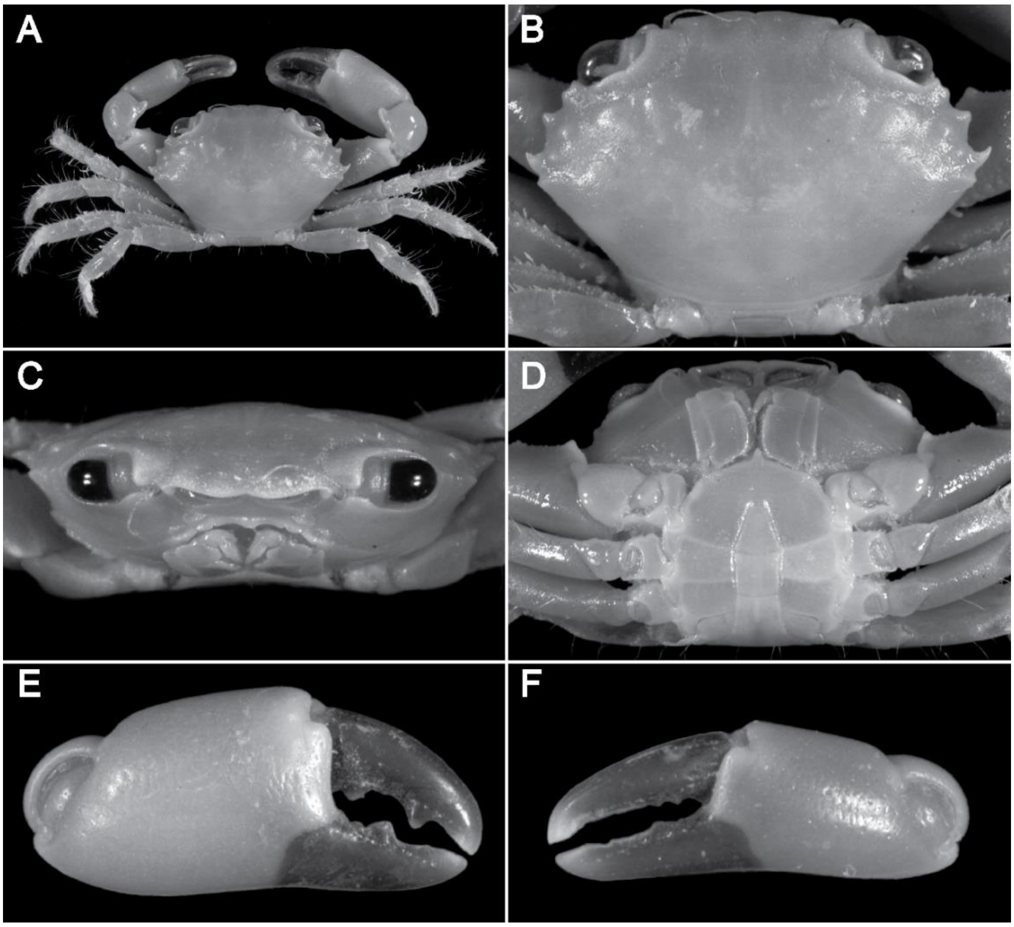


Plate 7. *Chlorodiella cytherea* (Dana, 1852) form 4, male, 9.6 × 6.2 (ZRC 2008.0644), Philippines; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

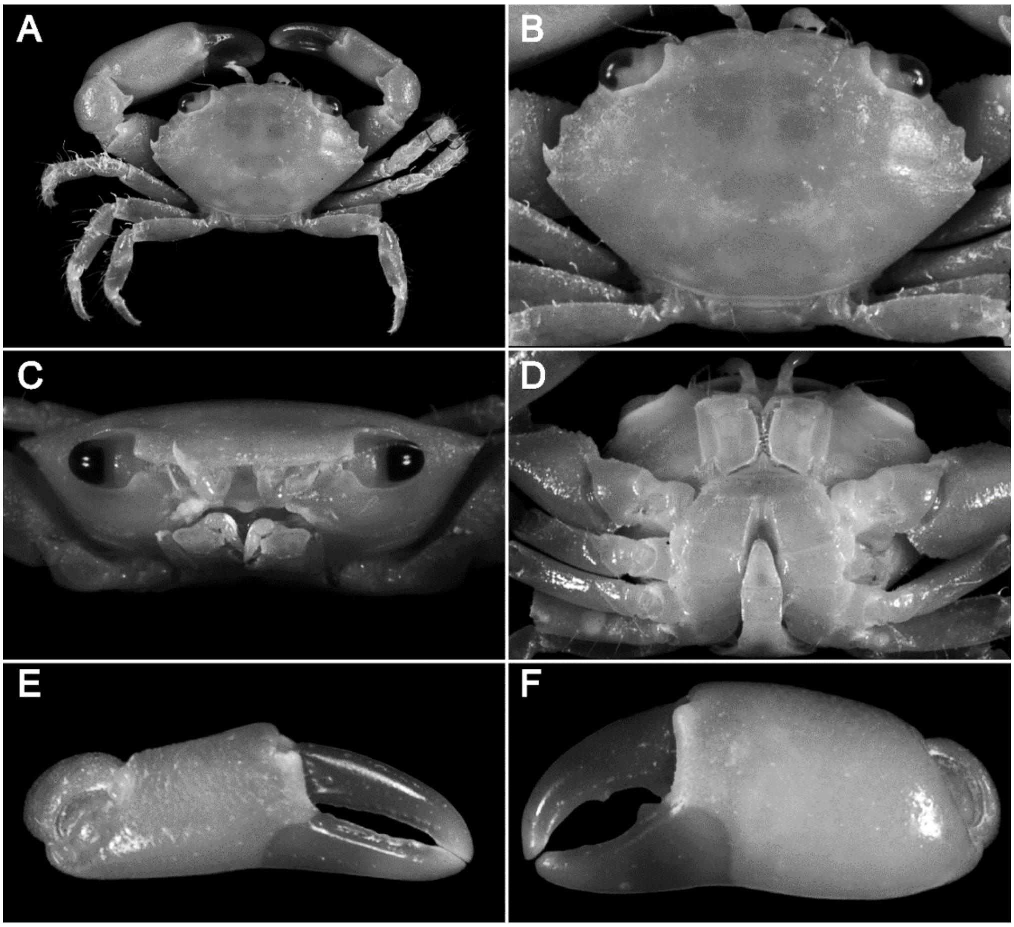


Plate 8. *Chlorodiella planapexa* sp. nov., male, 6.5 × 4.1 (UF 13733), Marshall Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

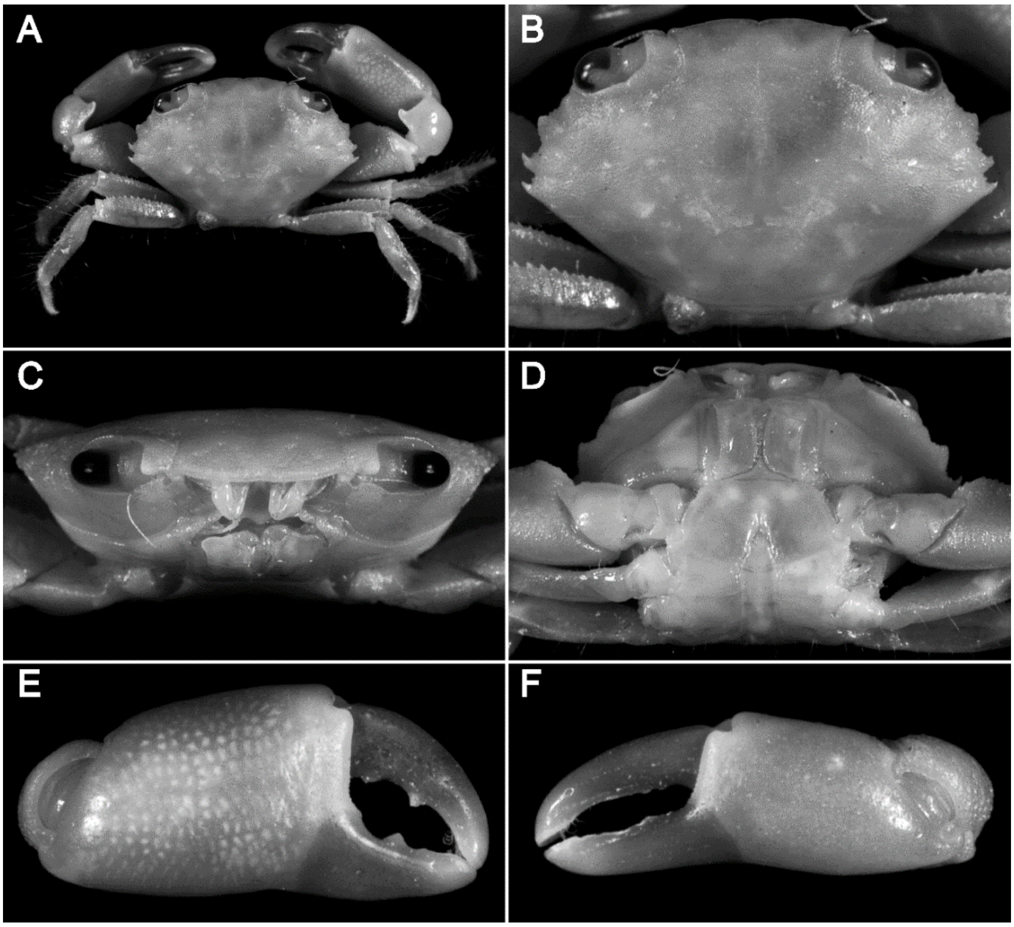


Plate 9. *Chlorodiella laevissima* (Dana, 1851), male, 8.7 × 5.3 (UF 13803), Line Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

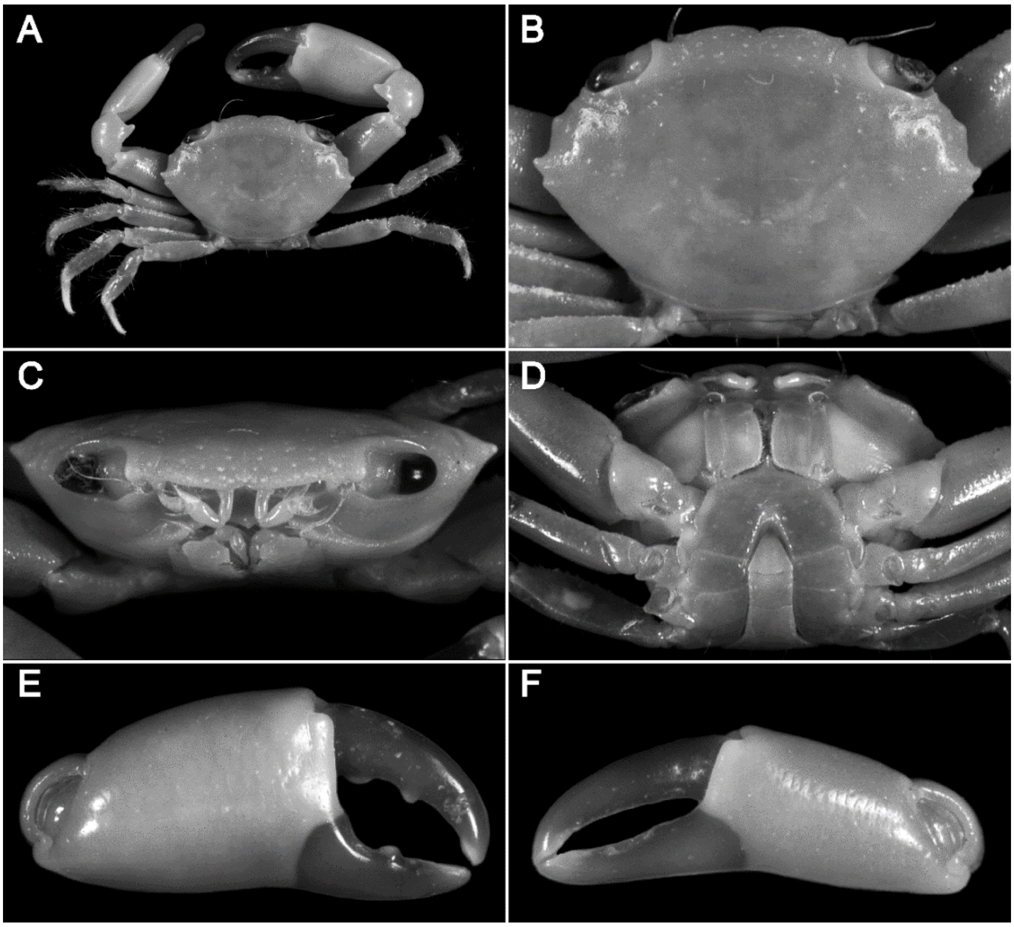


Plate 10. *Chlorodiella martensi* (Krauss, 1843), male, 9.0 × 5.9 (UF 9966), Moorea; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

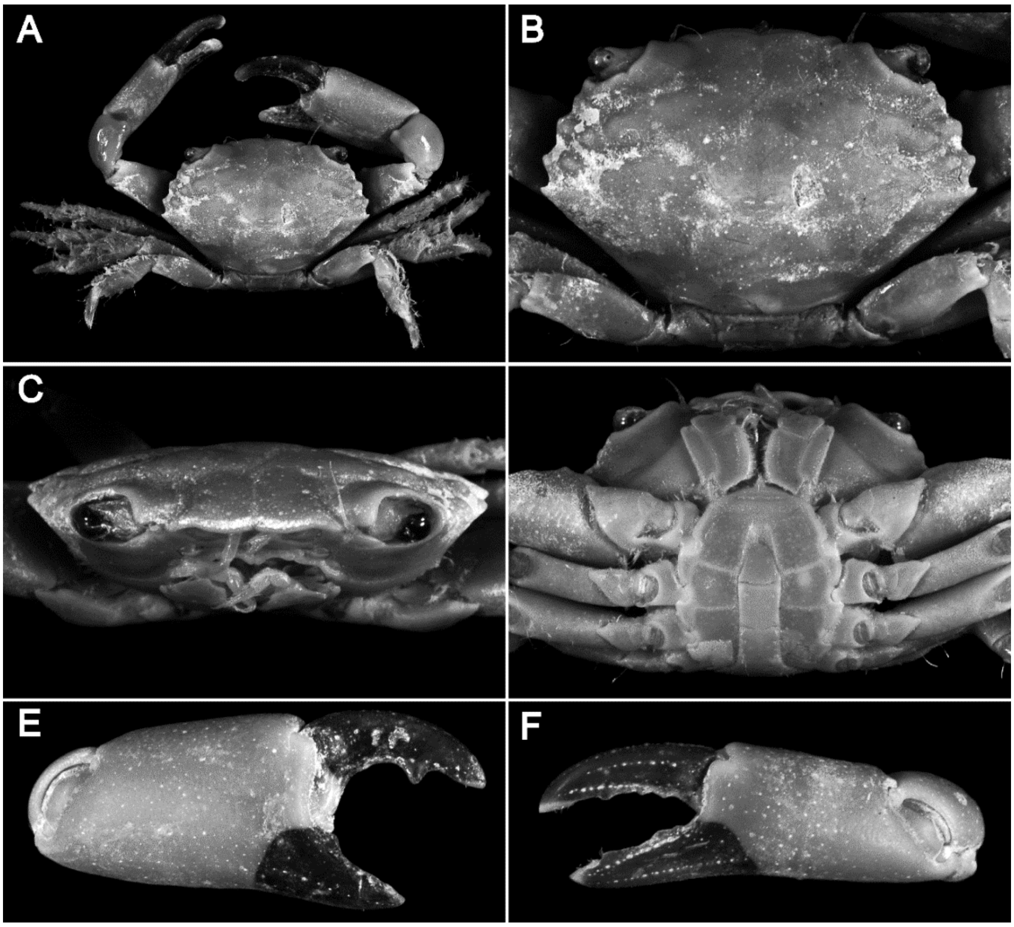


Plate 11. *Chlorodiella nigra* (Forskål, 1775) form 1, male, 16.85 × 11.05 (SMF 7161), Red Sea; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

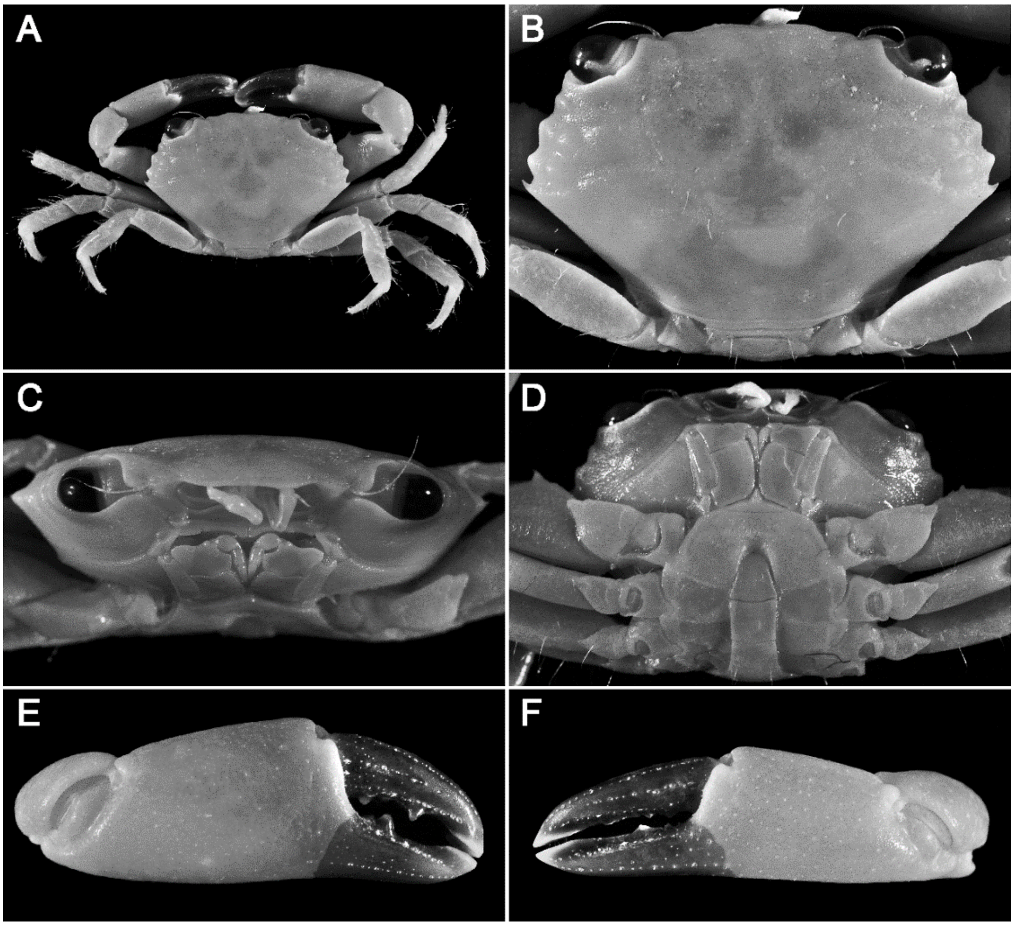


Plate 12. *Chlorodiella nigra* (Forskål, 1775) form 2, male, 13.0 × 8.6 (UF 3014), Guam; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

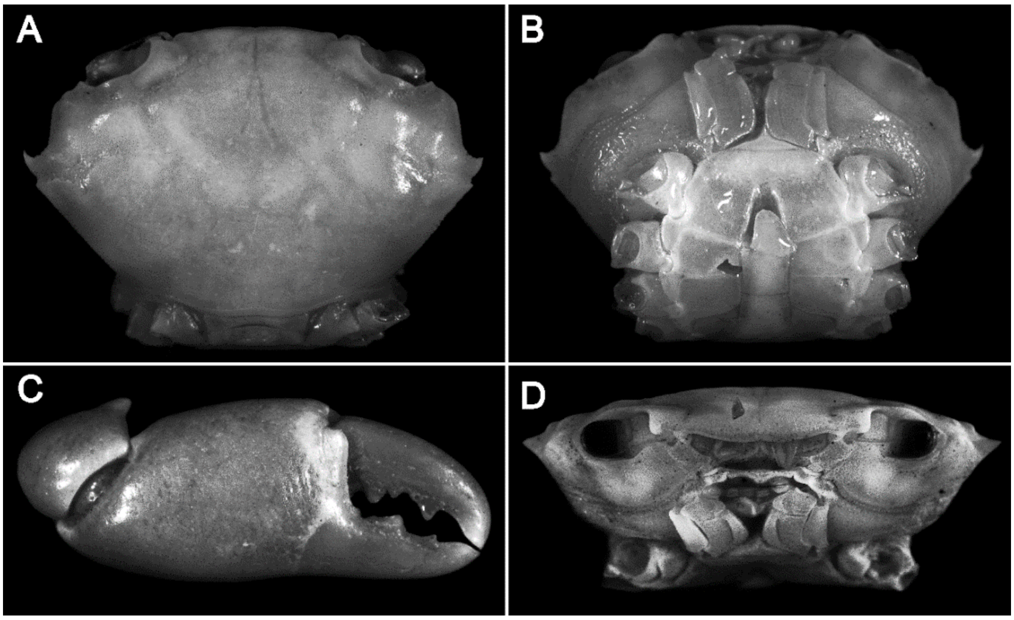


Plate 13. *Chlorodiella ohshimai* (Miyake & Takeda, 1976), holotype male, 12.55 × 7.85 (ZLKU 2613), Guam; *A*, carapace, dorsal view; *B,* thoracic sternum; *C*, major chela, external view; *D,* frontal view.

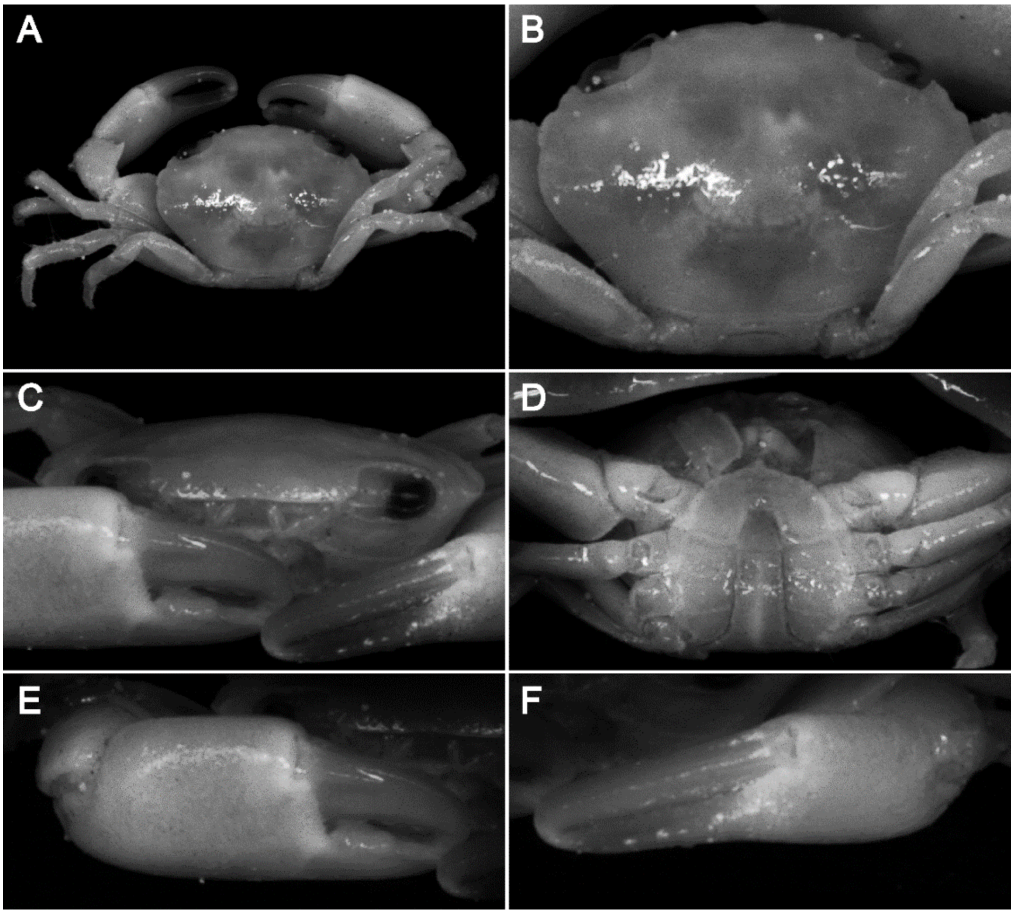


Plate 14. *Chlorodiella quadrilobata* (Dai, Cai & Yang, 1996), type female (CB 03282), Guam; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

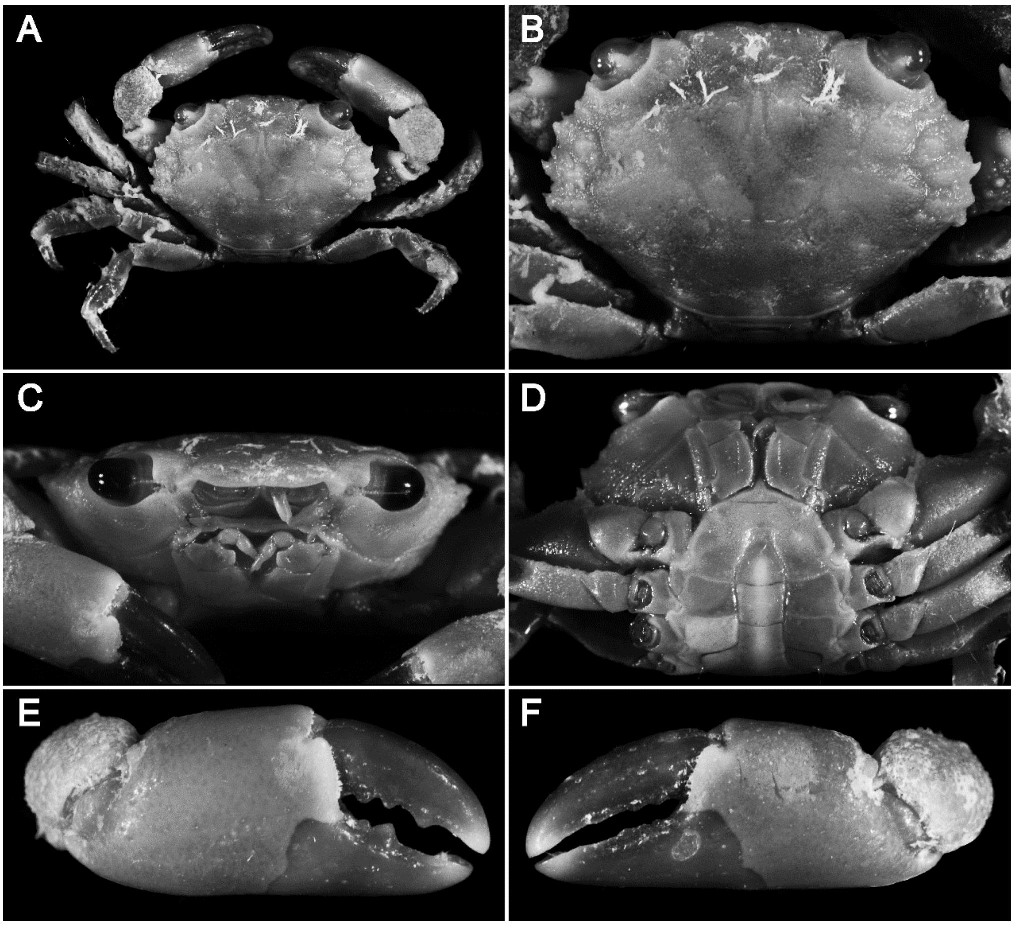


Plate 15. *Chlorodiella xishaensis* Chen & Lan, 1978, male, 9.19 × 6.52 (USNM 65177), Philippines; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

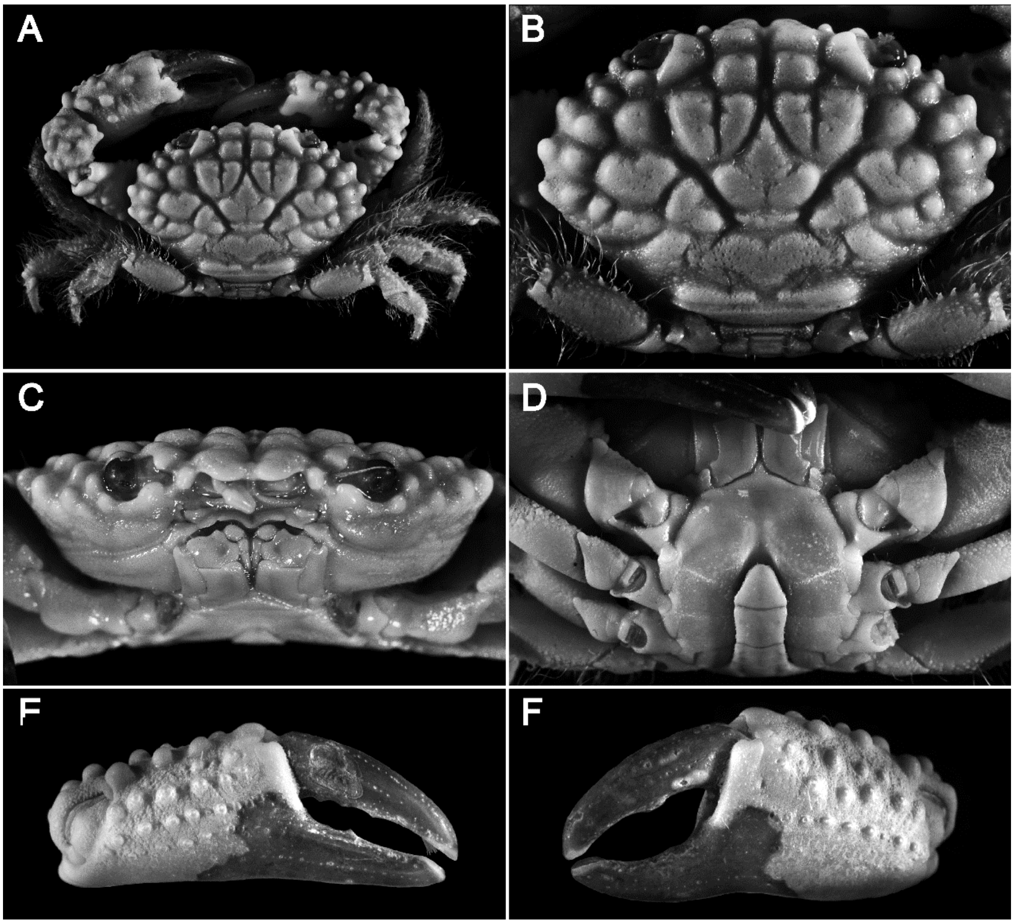


Plate 16. *Cyclodius drachi* (Guinot, 1964), holotype male, 15.9 × 10.6 (MNHN-B13117), Madagascar; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

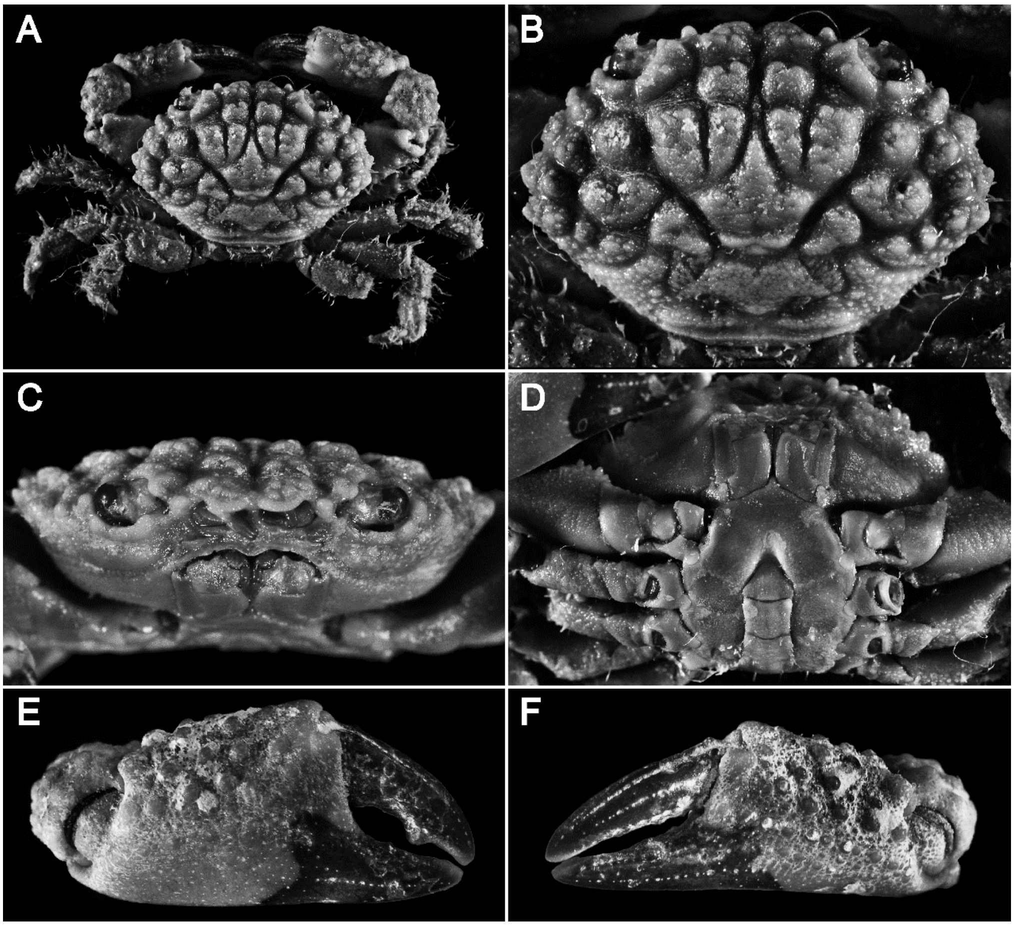


Plate 17. *Cyclodius granulatus* (Targioni-Tozzetti, 1877), male, 16.1 × 11.2, (MNHN B6776), Djibouti; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

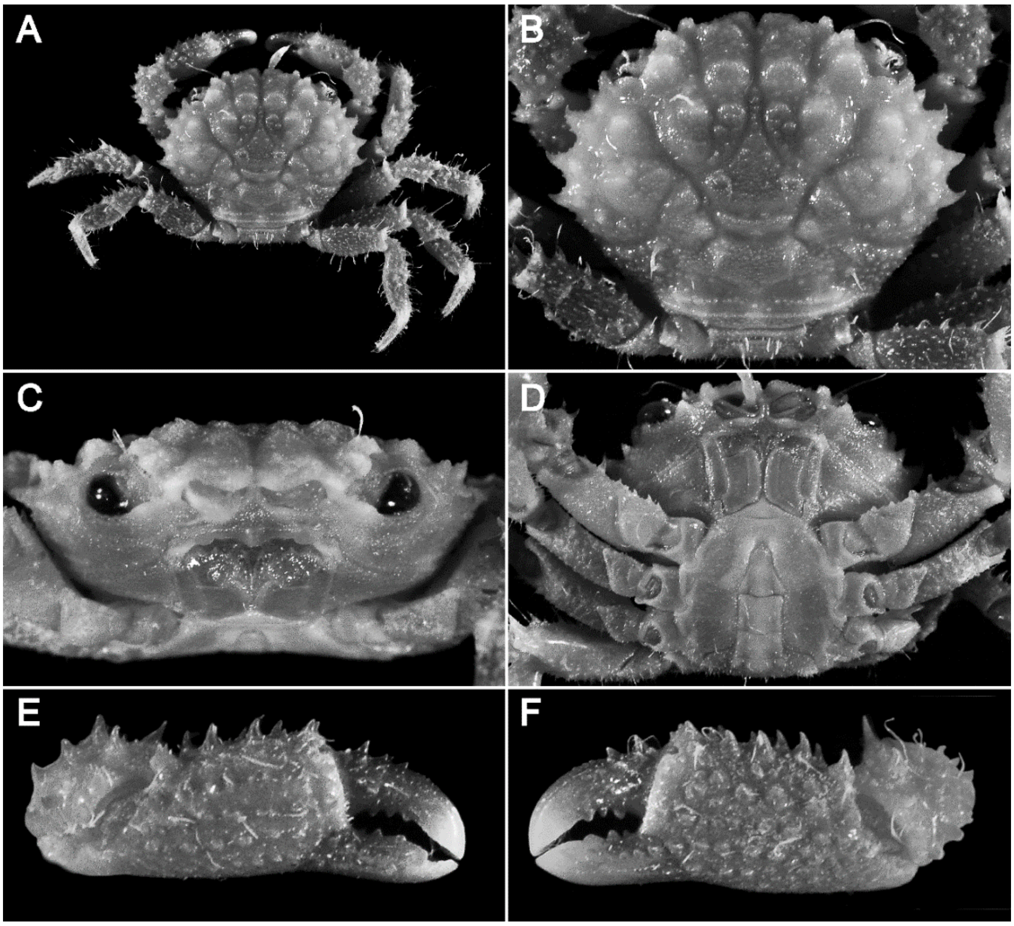


Plate 18. *Cyclodius granulosus* De Man, 1888, male, 7.9 × 6.0, (UF 3017), Guam; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

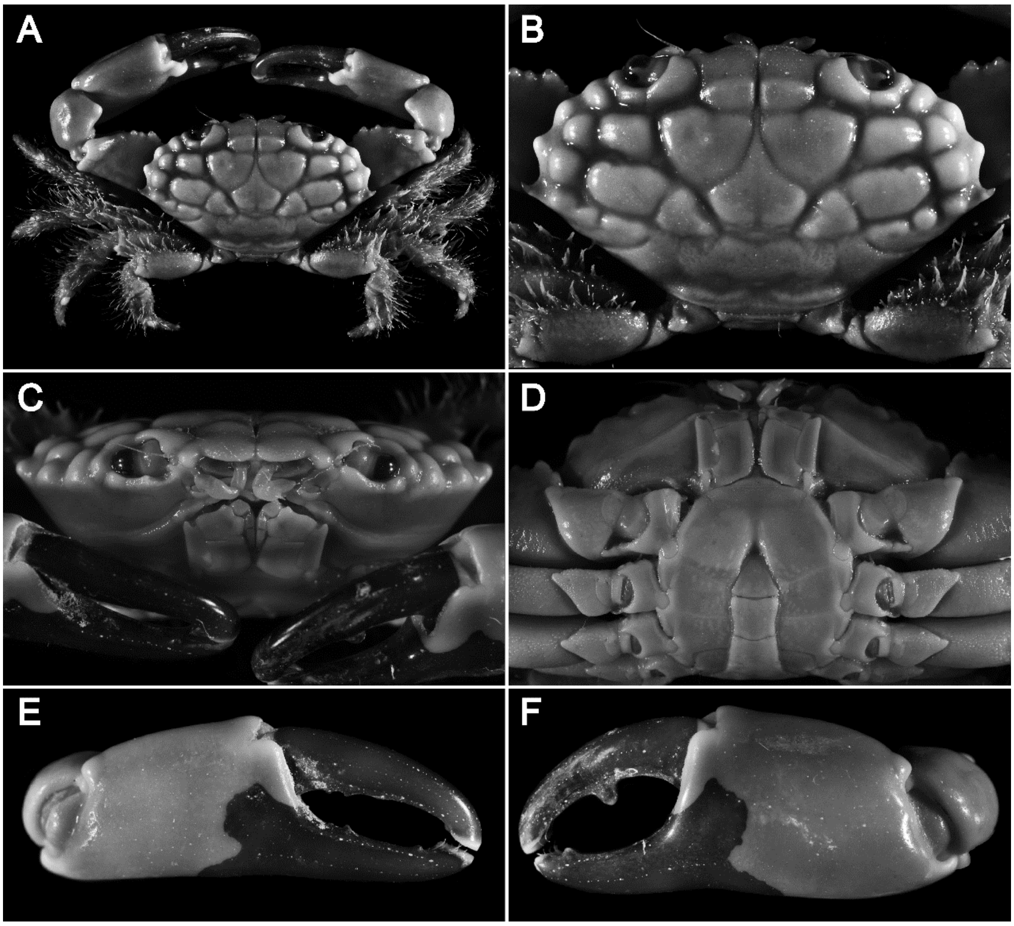


Plate 19. *Cyclodius nitidus* (Dana, 1852) form 1, male, 23.8 × 14.3, (USNM 154905), Western Samoa; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

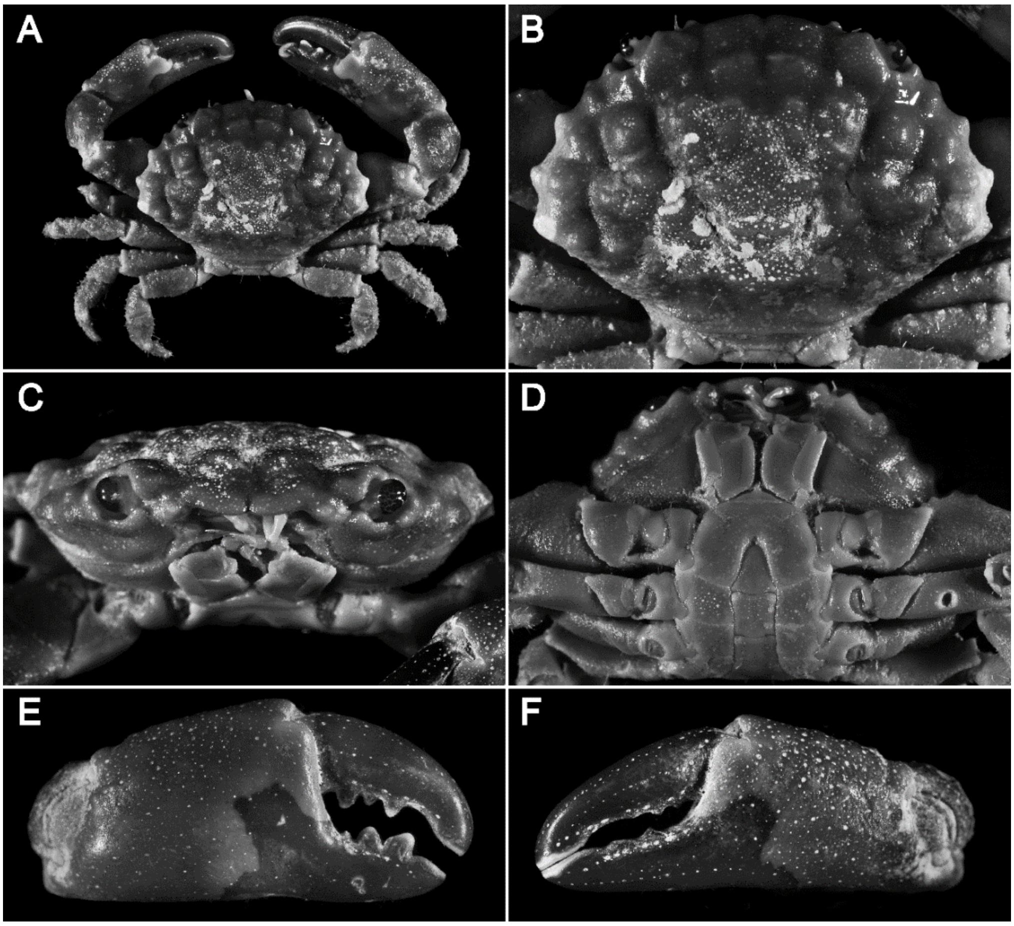


Plate 20. *Cyclodius obscurus* (Hombron & Jacquinot, 1846), male, 24.5 × 17.9, (USNM 91638), Western Samoa; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

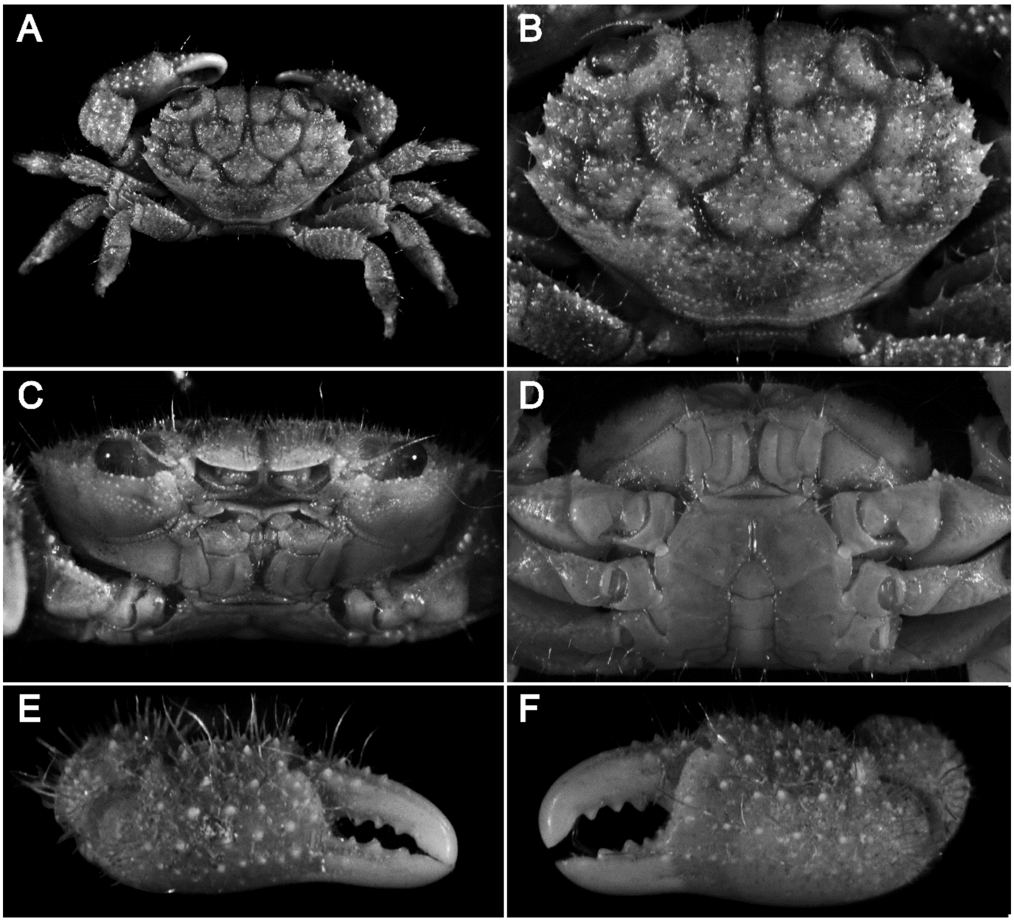


Plate 21. *Cyclodius paumotensis* (Rathbun, 1907), holotype male, 7.9 × 5.2 (USNM 32852), Tuamotu Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

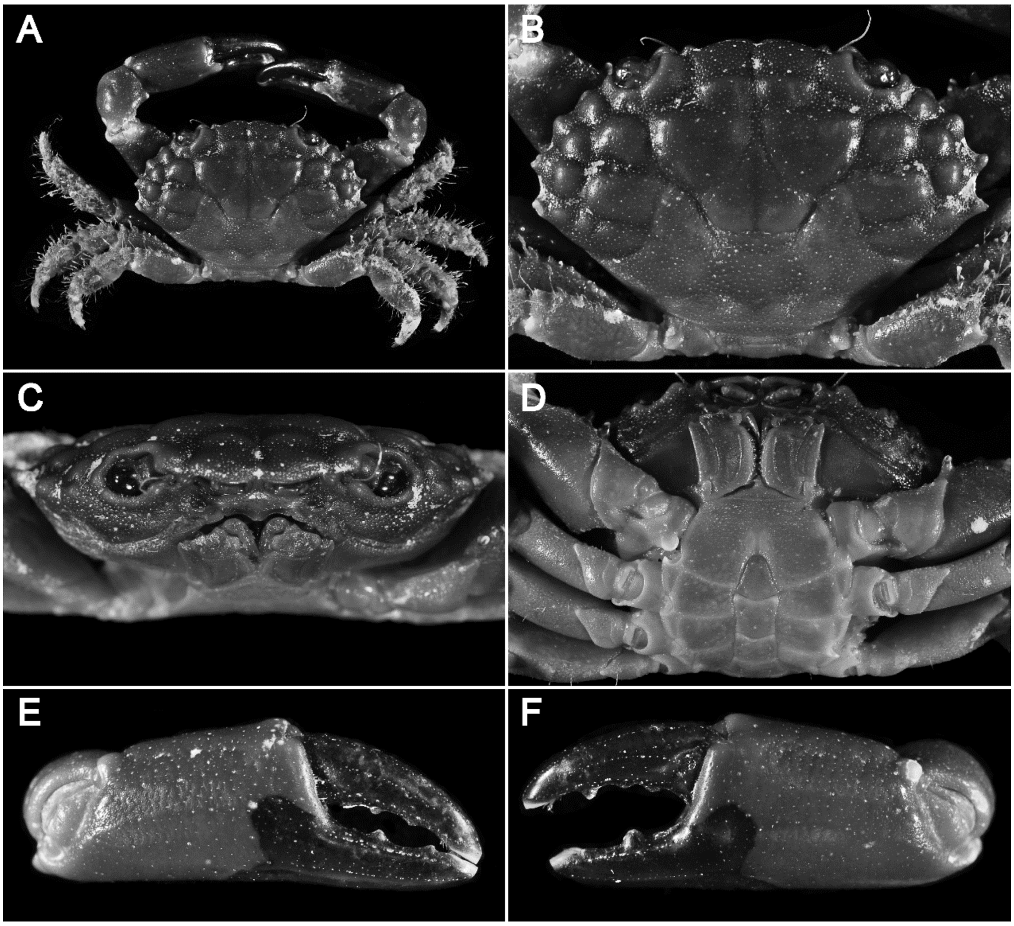


Plate 22. *Cyclodius nitidus* (Dana, 1852) form 2, male, 18.6 × 12.2 (UF 33025), Red Sea; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

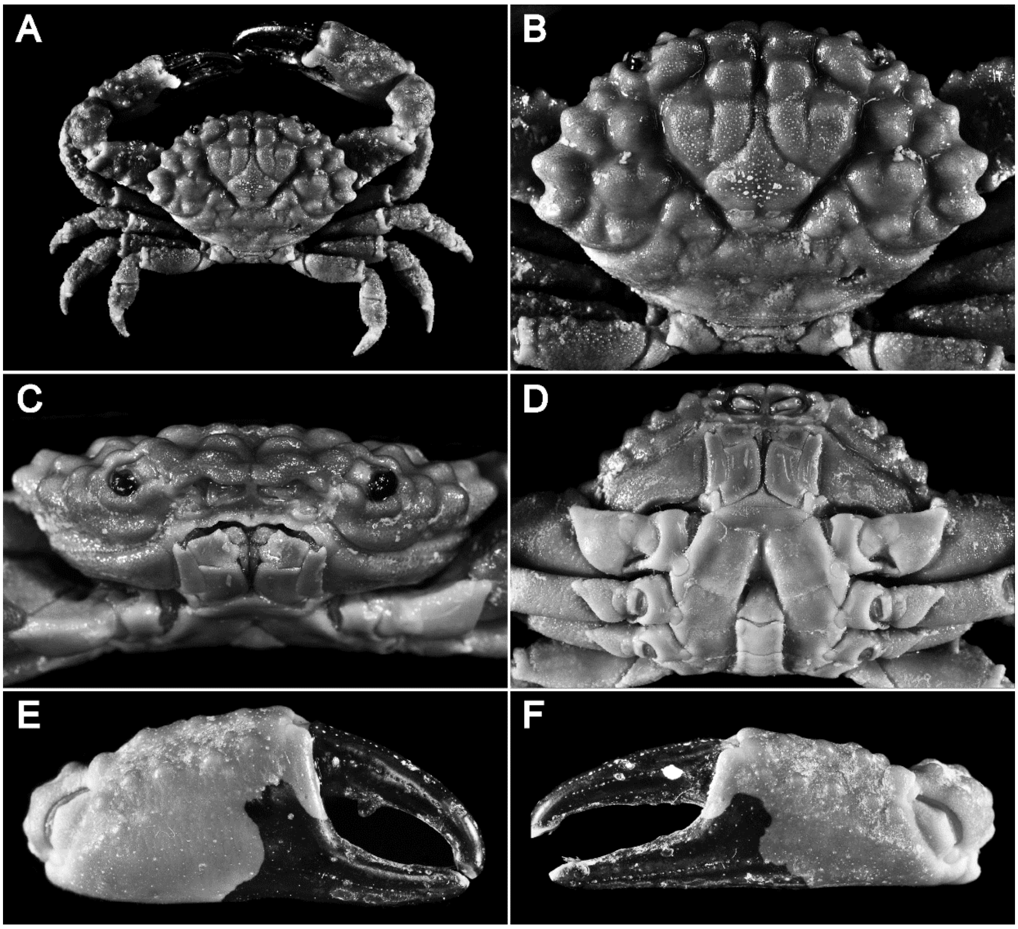


Plate 23. *Cyclodius ungulatus* (H. Milne Edwards, 1834), male, 25.3 × 17.2 (USNM 1181301), Great Barrier Reef; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

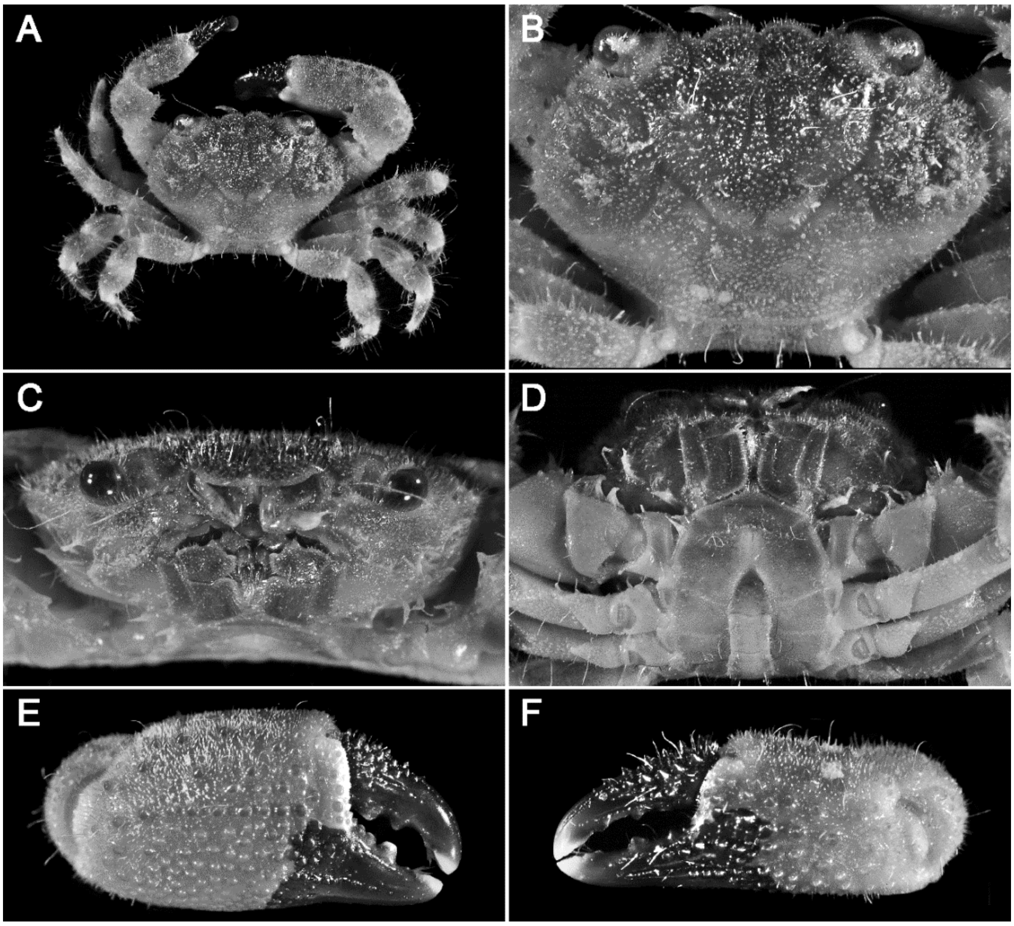


Plate 24. *Luniella pubescens* (Dana, 1852), male, 13.2 × 8.6, (ZRC 2013.1654), Japan; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

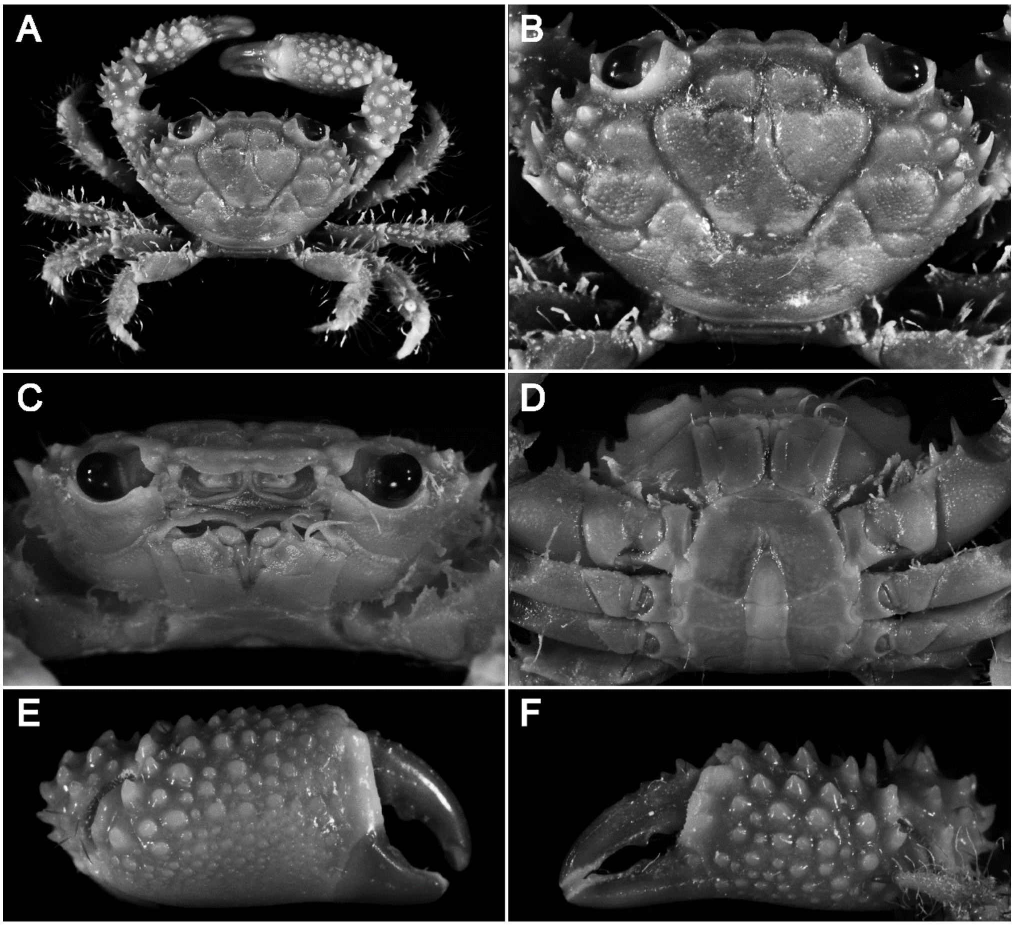


Plate 25. *Luniella pugil* (Dana, 1852), male, 11.2 × 7.2, (USNM 33412), Society Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

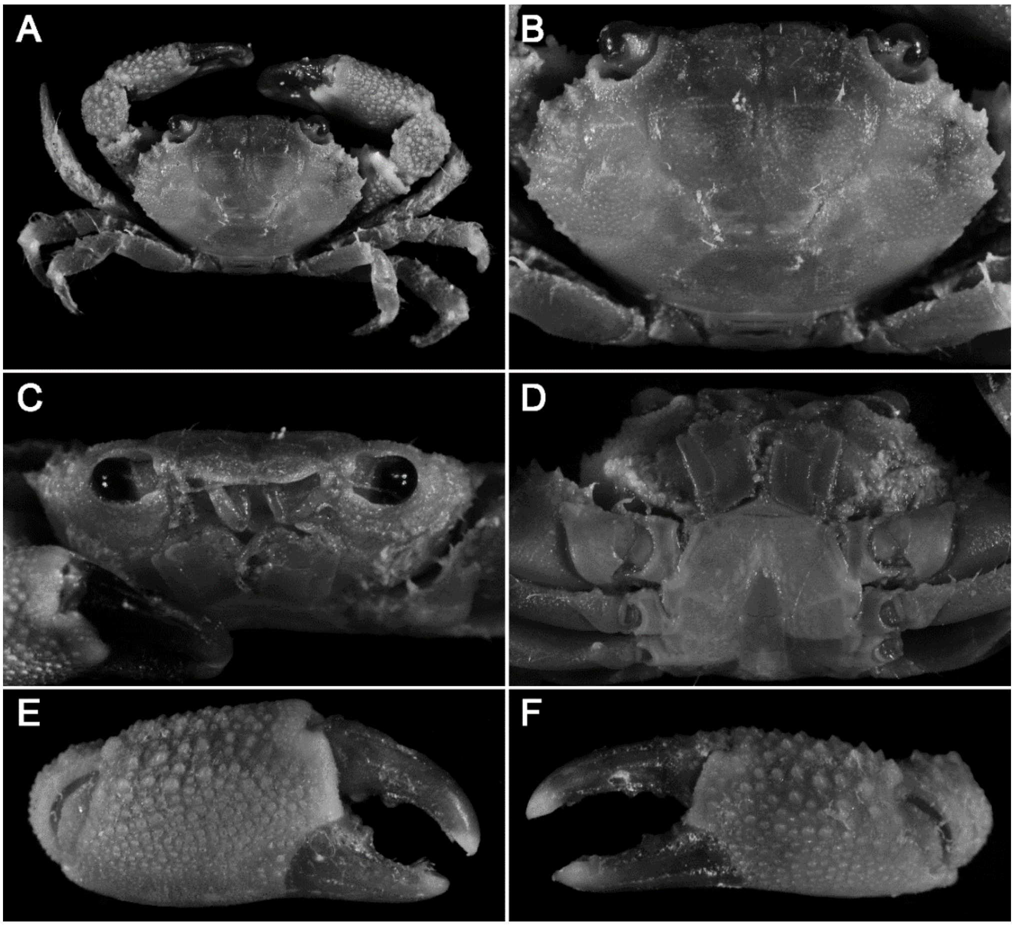


Plate 26. *Luniella scabricula* (Dana, 1852), male, 9.0 × 5.8, (USNM 1181460), Marshall Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

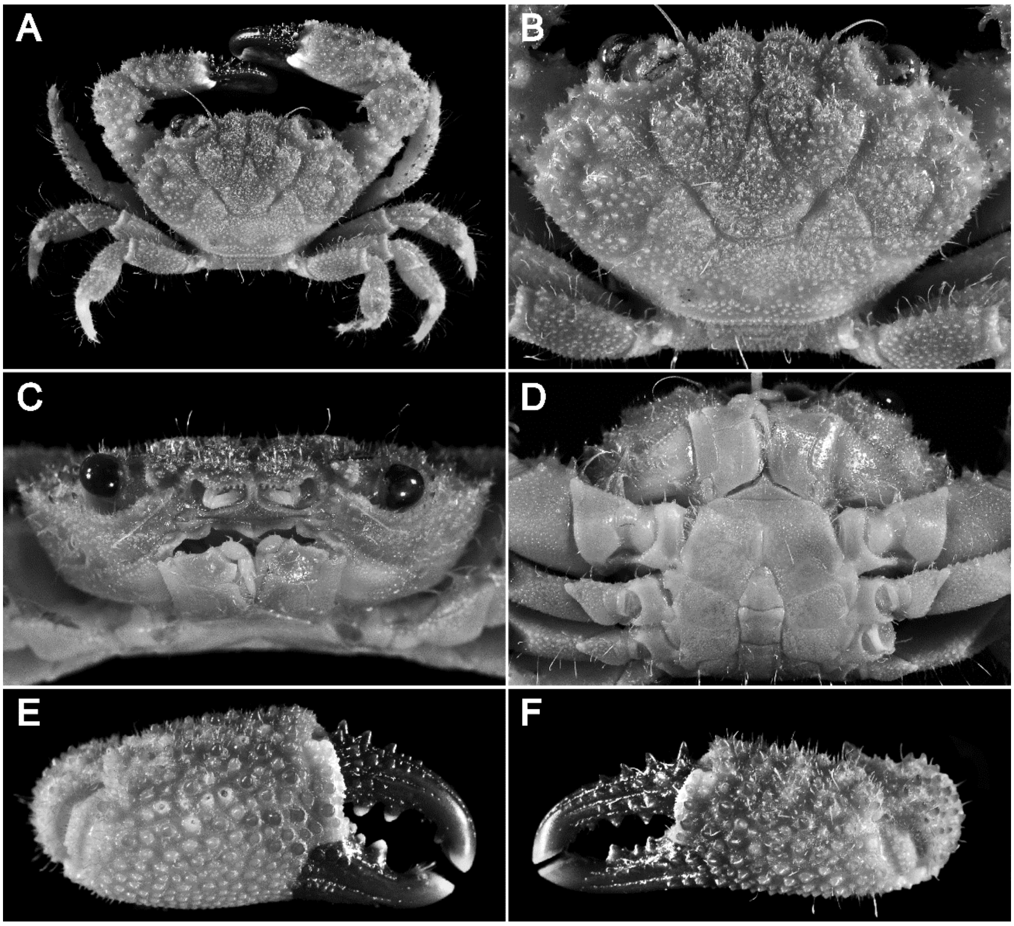


Plate 27. *Luniella spinipes* (Heller, 1861), male, 15.3 × 10.1, (UF 14361), Madagascar; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

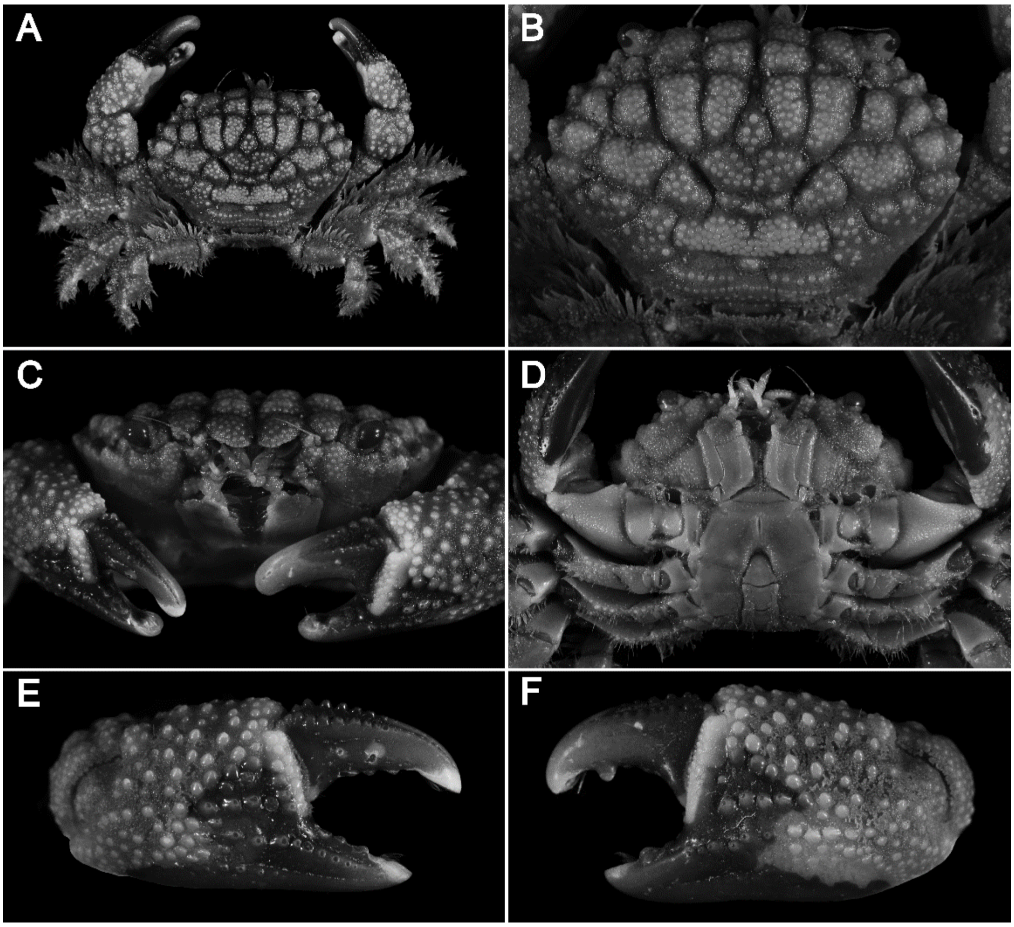


Plate 28. *Pilodius areolatus* (H. Milne Edwards, 1834), male, 15.2 × 10.9, (UF 99146), Hawaiian Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

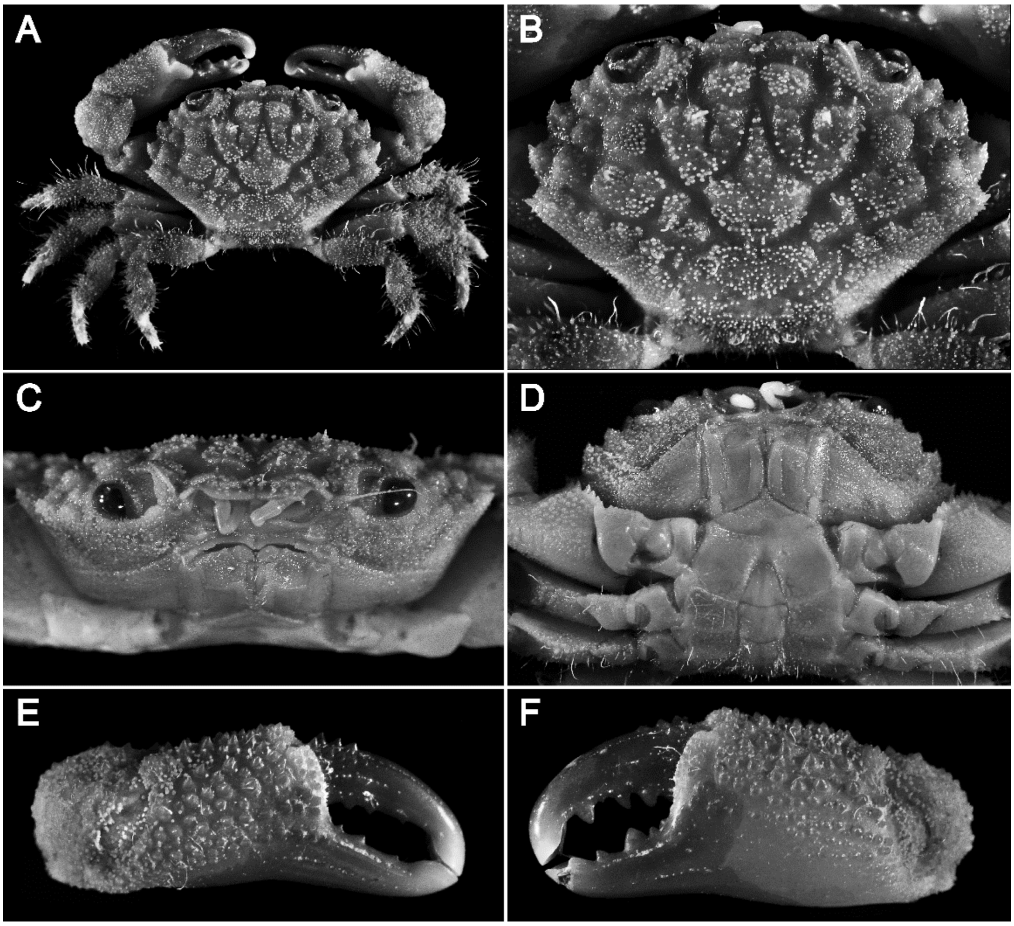


Plate 29. *Pilodius granulatus* Stimpson, 1859, male, 11.90 × 8.00, (ZRC 1989.3436), Singapore; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

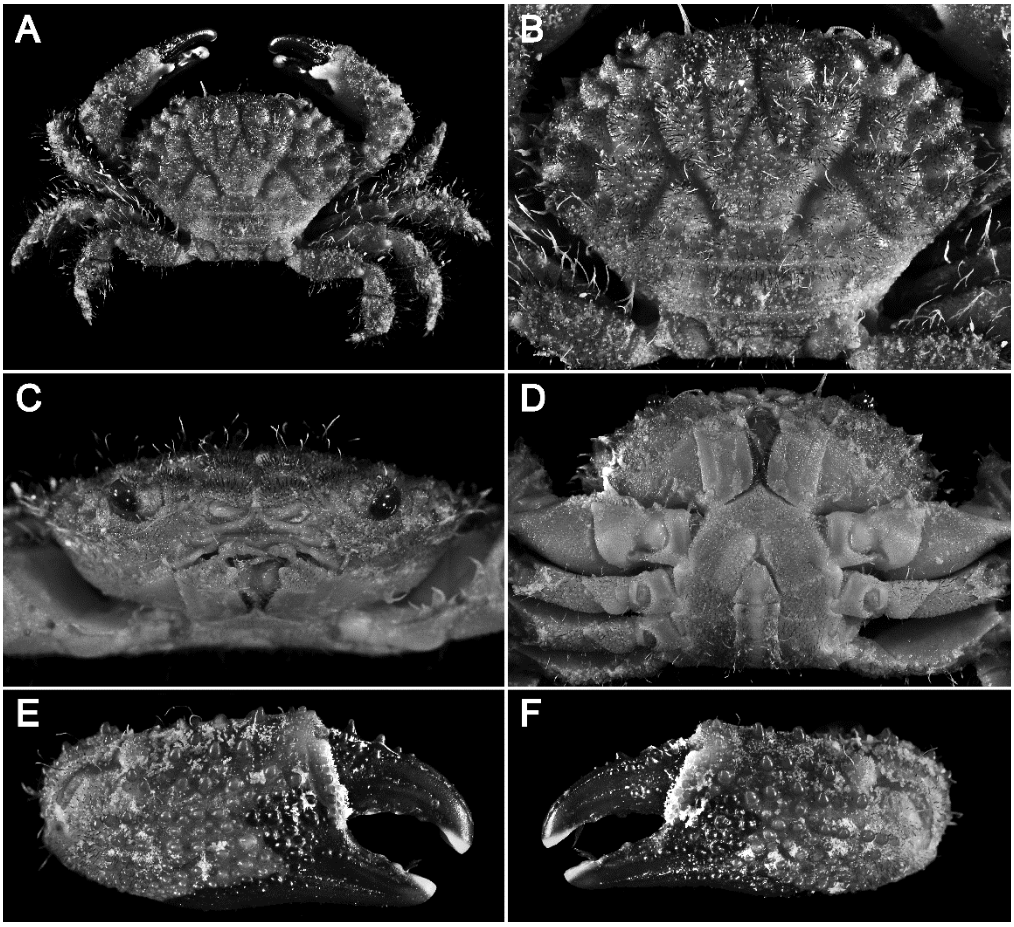


Plate 30. *Pilodius maotieni* Serène, 1971, male, 19.8 × 13.1 (ZRC 2013.1645), Vanuatu; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

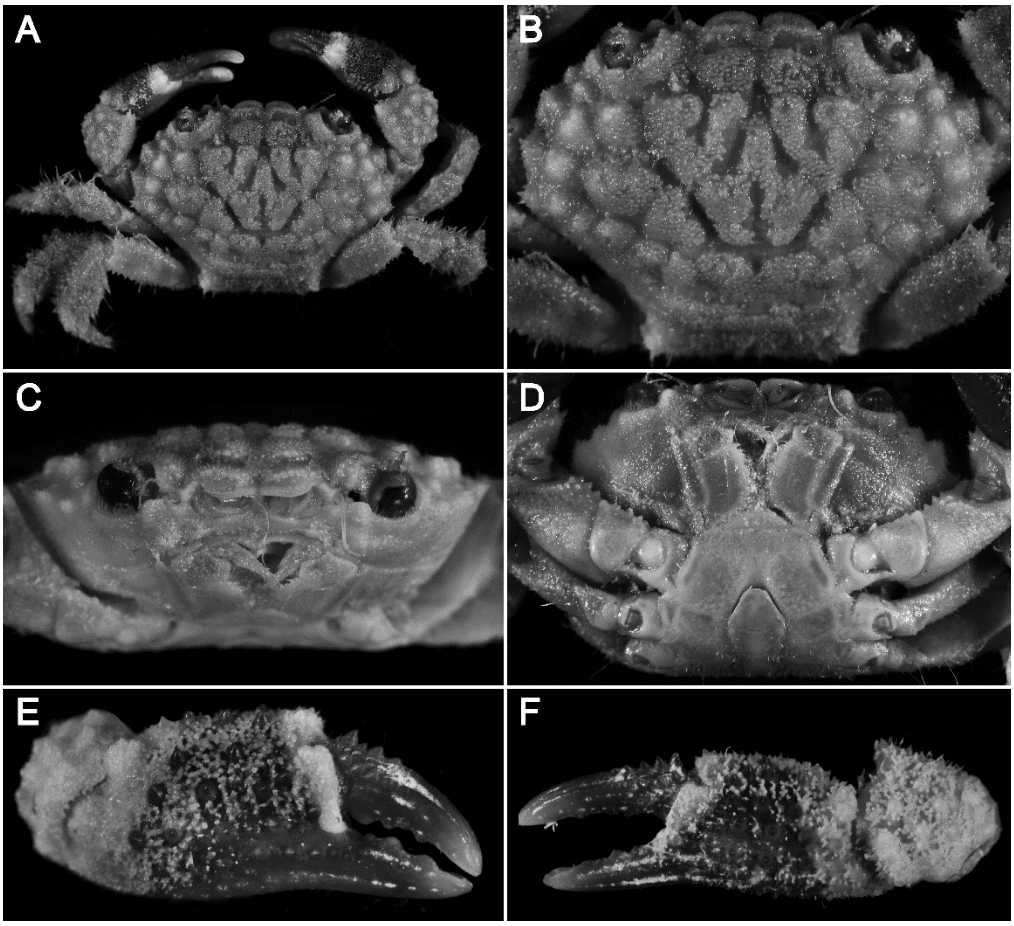


Plate 31. *Pilodius miersi* (Ward, 1936), male, 11.2 × 7.7 (USNM 65283), Philippines; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

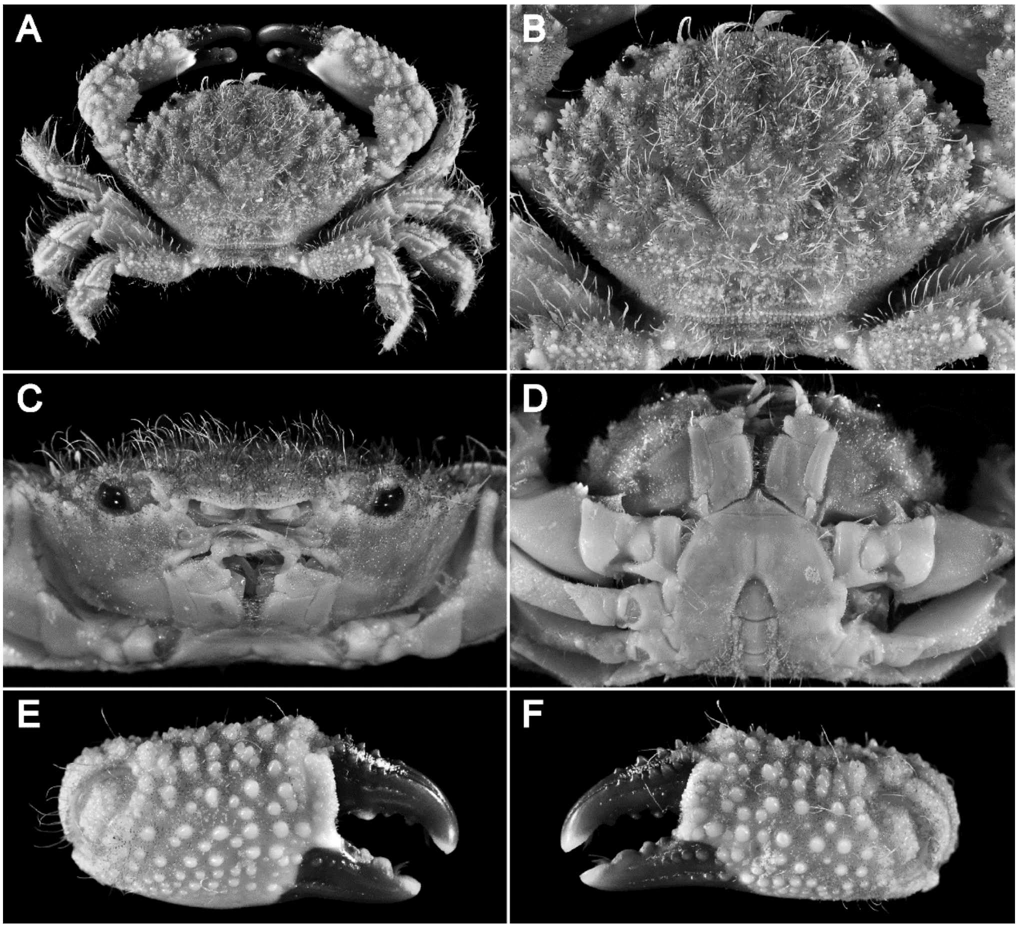


Plate 32. *Pilodius moranti* Clark & Galil, 1993, male, 21.0 × 14.3 (QM 15454), Coral Sea; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

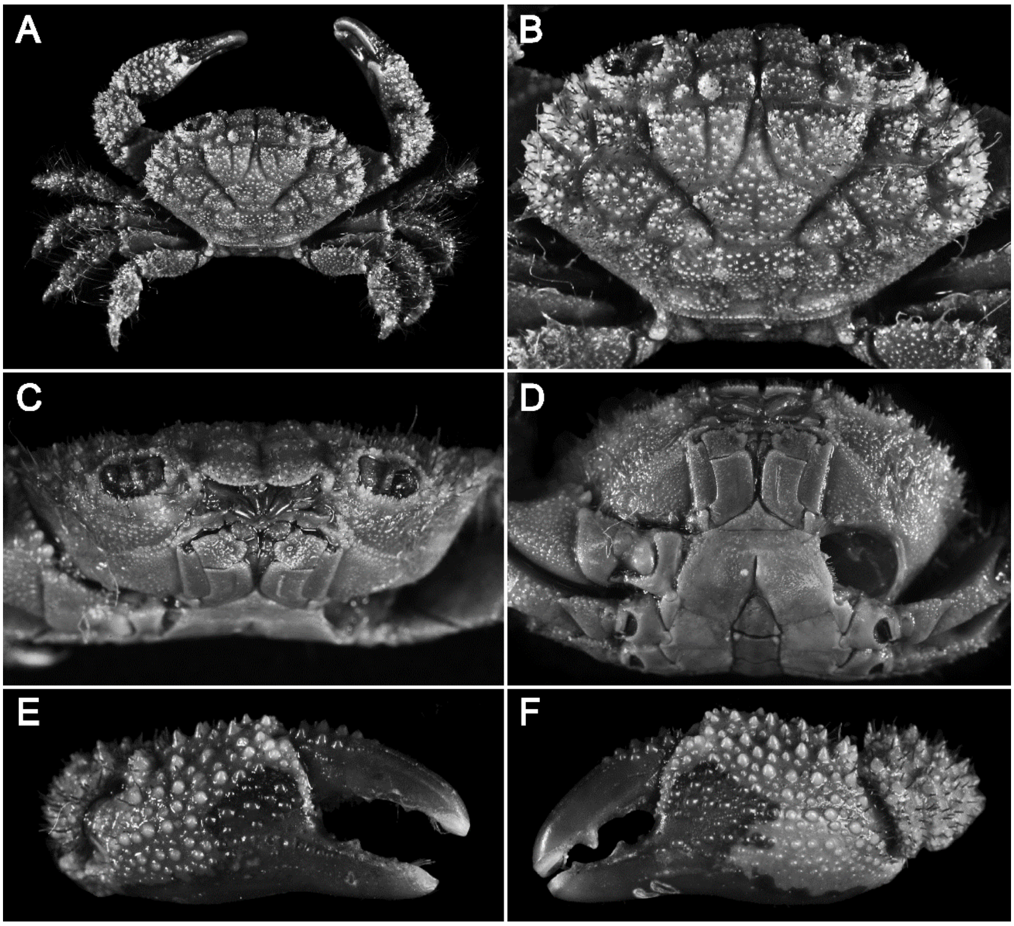


Plate 33. *Pilodius nigrocrinitus* Stimpson, 1859, male (USNM 20293), New Caledonia; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

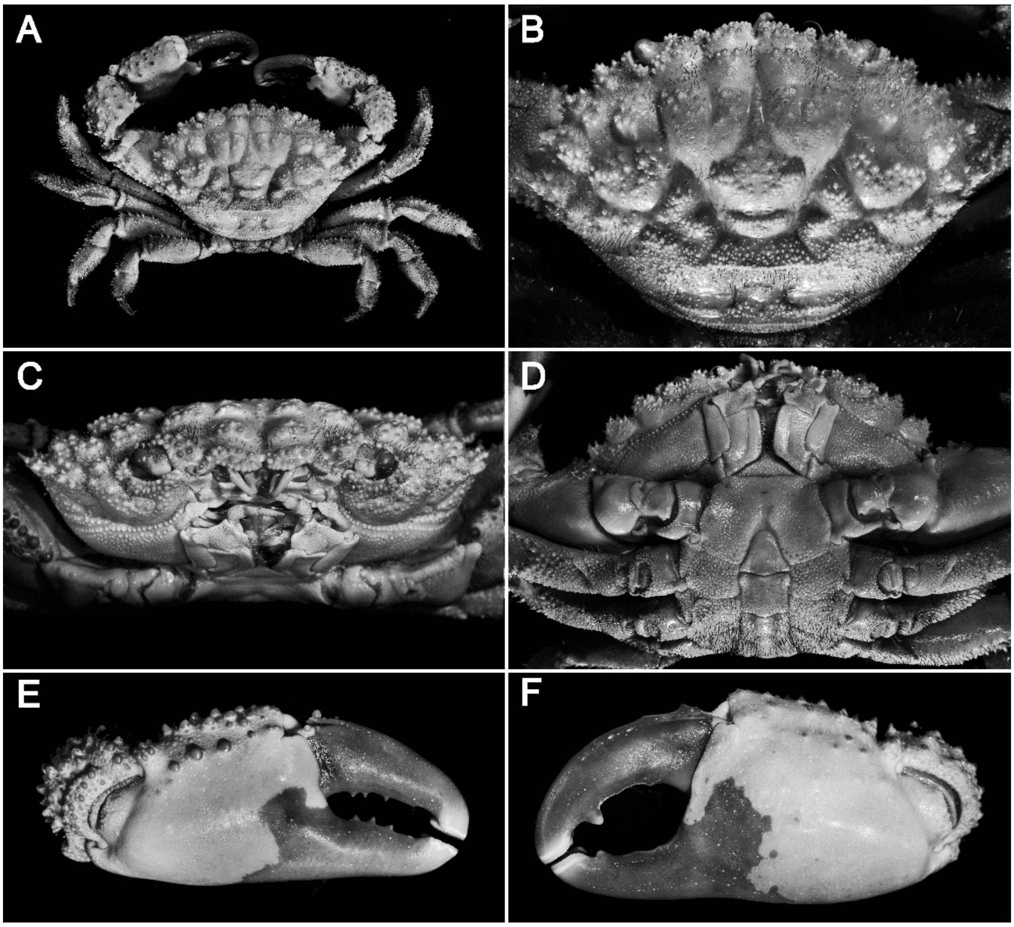


Plate 34. *Pilodius pilumnoides* (White, 1848), male, 62.25 × 42.00 (ZRC 1965.11.11.147), Singapore; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

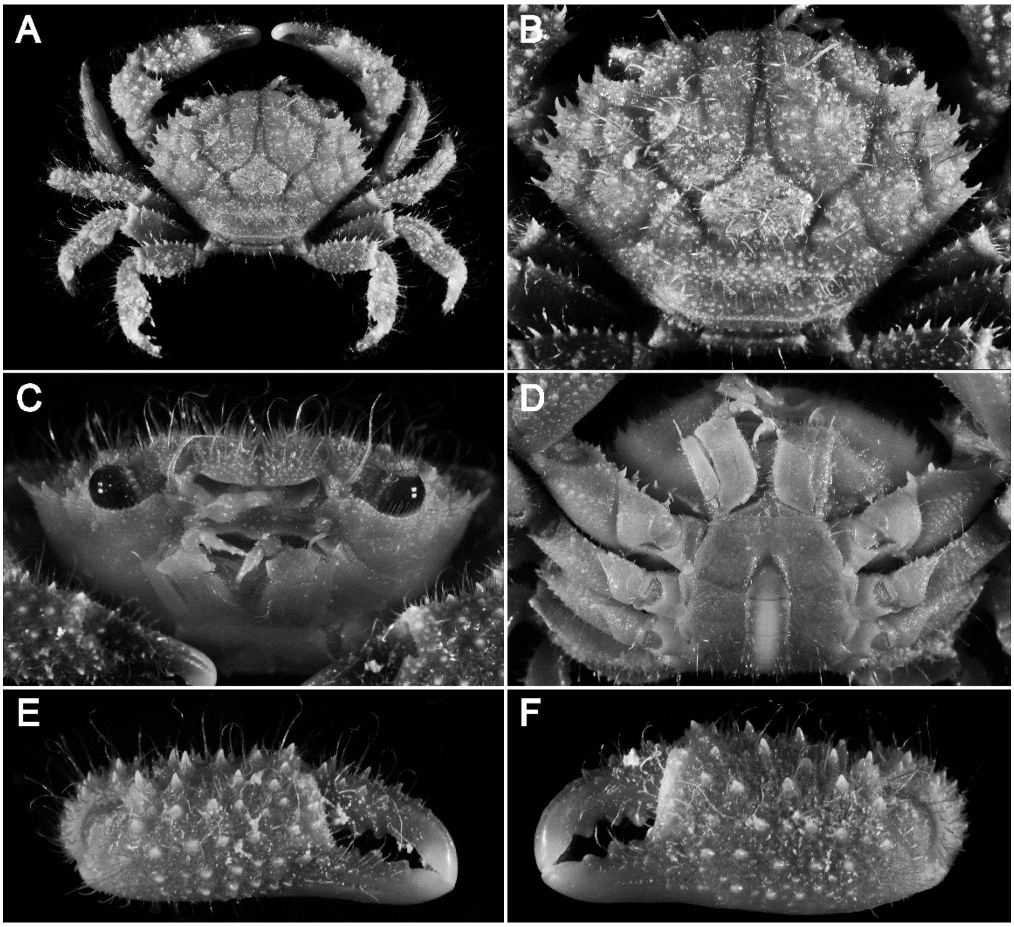


Plate 35. *Soliella flava* (Rathbun, 1894), male, 10.2 × 6.9 (USNM 1181377), Marshall Islands; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, minor chela, external view; *F*, major chela, external view.

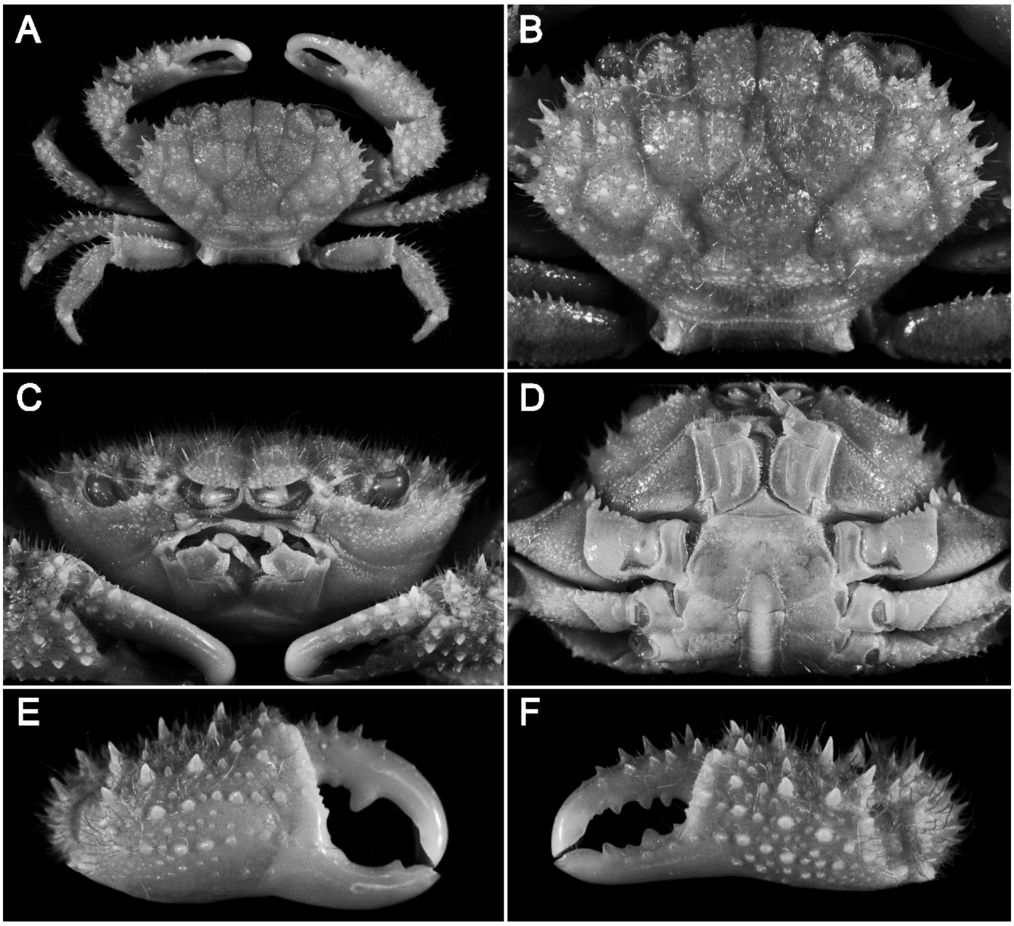


Plate 36. *Soliella melanospinis* (Rathbun, 1911), holotype male, 17.0 × 11.4 (USNM 41268), Saya del Malha Bank; *A*, dorsal view; *B*, carapace, dorsal view; *C*, frontal view; *D*, thoracic sternum; *E*, major chela, external view; *F*, minor chela, external view.

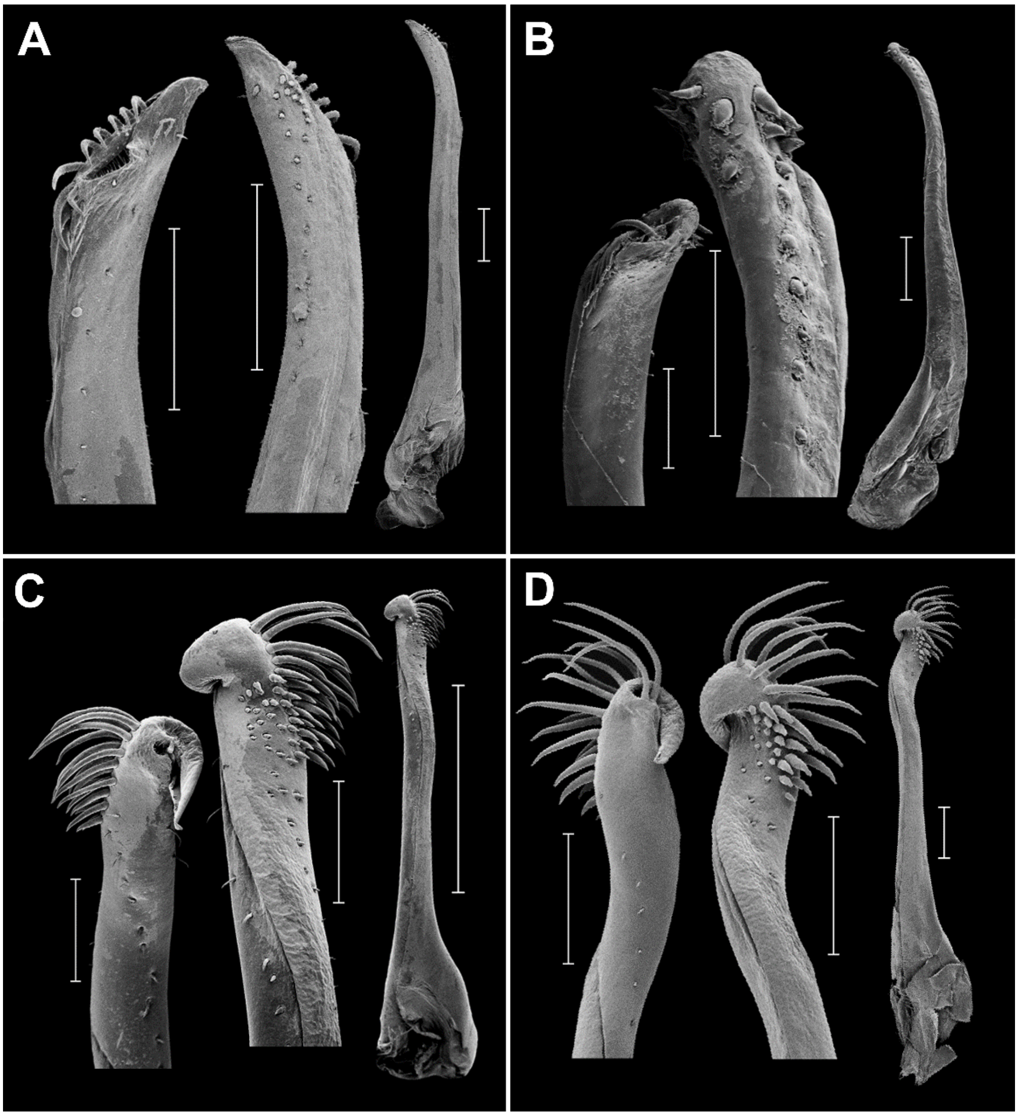


Plate 37. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Chlorodiella barbata* (Borradaile, 1900), right G1, 200um, 200um, 200um (UF 25049); B – *Chlorodiella cochlearis* (Zehntner, 1894), right G1, 100um, 100um, 200um (USNM 155977); C – *Chlorodiella cytherea* (Dana, 1852) form 1, right G1 (reflected), 200um, 200um, 1mm (ZRC 2010.0373); D – *Chlorodiella cytherea* (Dana, 1852) form 5, right G1, 200um, 200um, 200um (UF 36830).

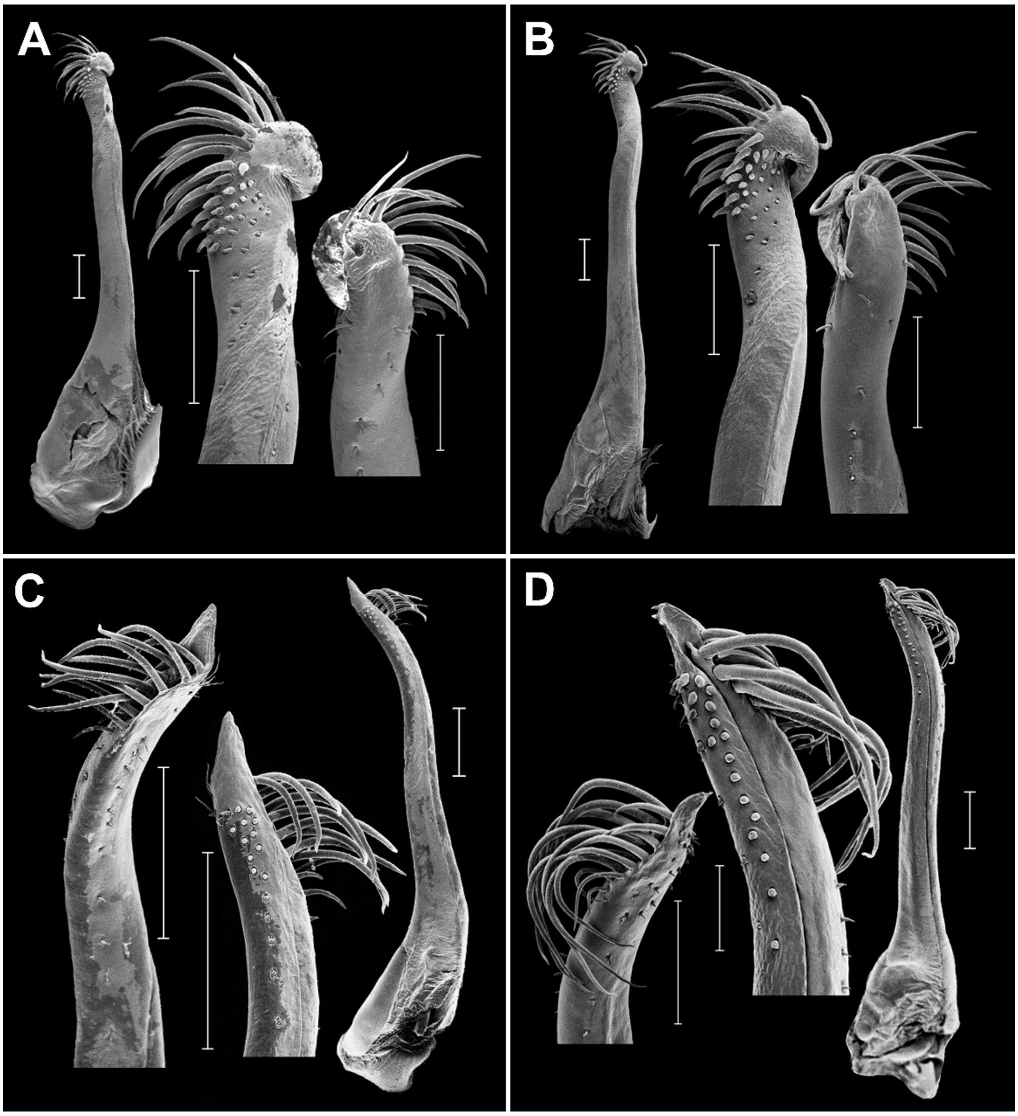


Plate 38. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Chlorodiella cytherea* (Dana, 1852) form 2, right G1, 200um, 200um, 200um (UF 2912); B – *Chlorodiella cytherea* (Dana, 1852) form 4, right G1, 200um, 200um, 200um (UF 17094); C – *Chlorodiella planapexa* sp. nov., right G1, 200um, 200um, 200m (UF 17841); D – *Chlorodiella laevissima* (Dana, 1852)., right G1, 200um, 100um, 200um (UF 13803).

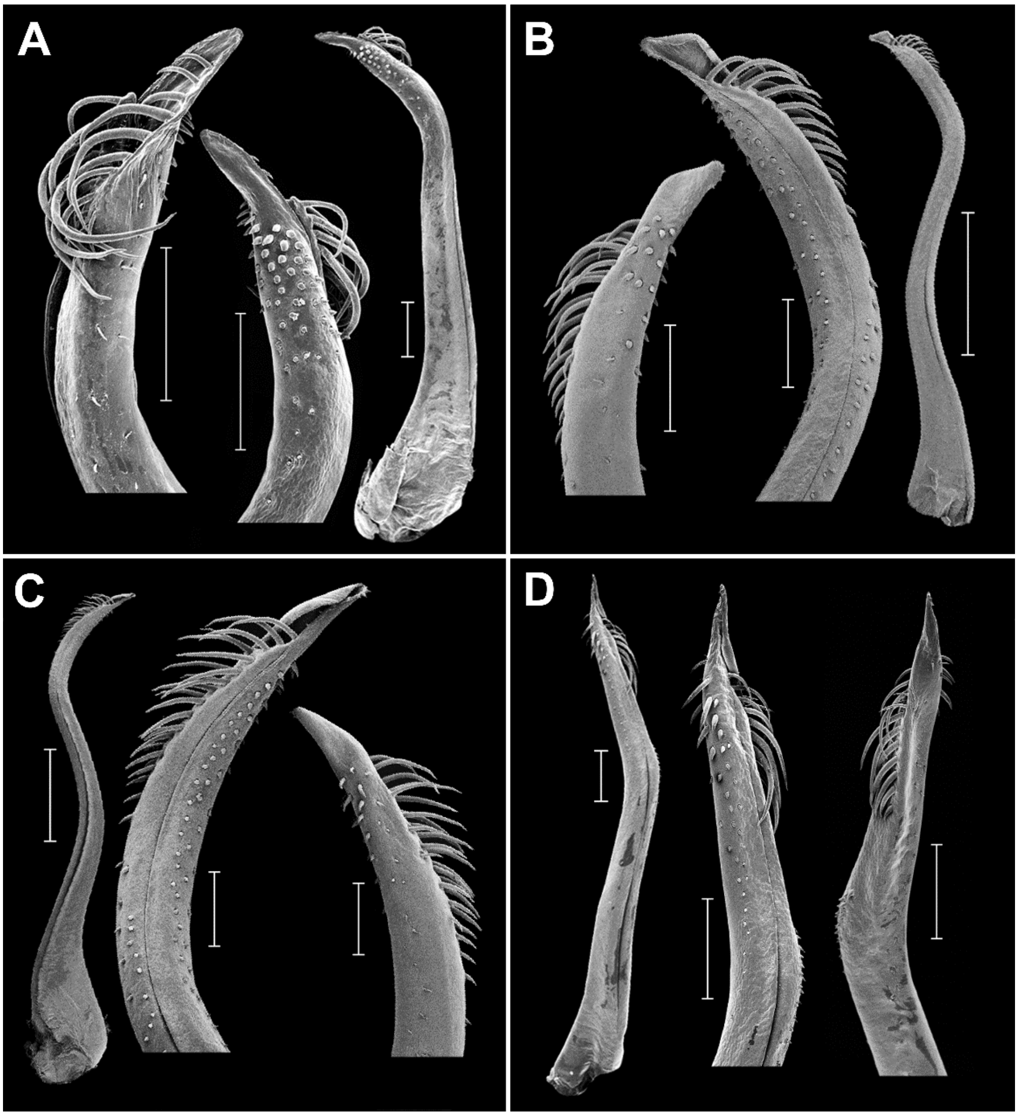


Plate 39. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Chlorodiella martensi* (Krauss, 1843), right G1, 200um, 200um, 200um (UF 11190); B – *Chlorodiella nigra* (Forskål, 1775) form 1, right G1, 200um, 200um, 1mm (UF 14275); C – *Chlorodiella nigra* (Forskål, 1775) form 2, left G1, 1mm, 200um, 200m (UF 5956); D – *Chlorodiella xishaensis* Chen & Lan, 1978, right G1, 200um, 200um, 200um (UF 25982).

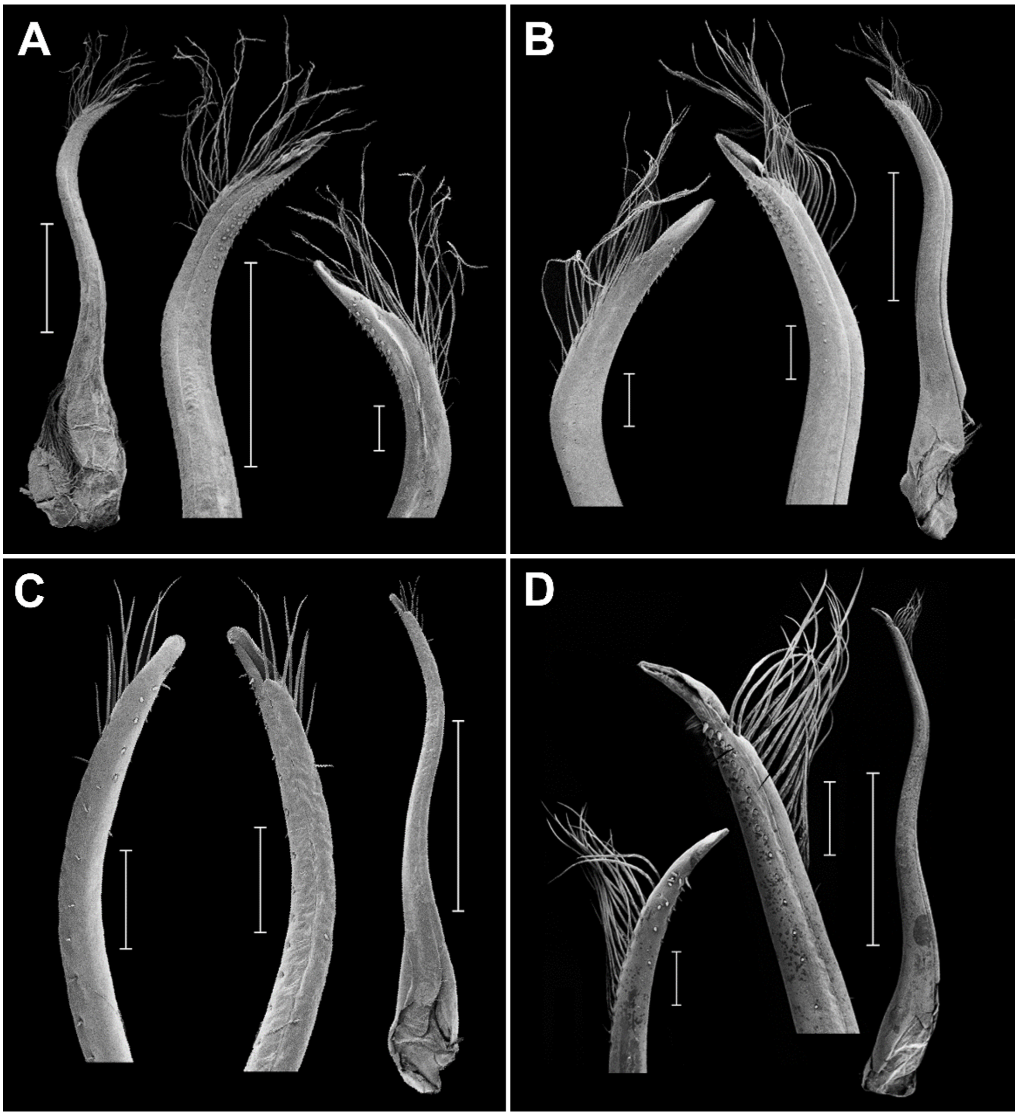


Plate 40. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Cyclodius drachi* (Guinot, 1964), left G1, 1mm, 1mm, 200um (MNHN-B13117); B – *Cyclodius granulatus* (Targioni-Tozzetti, 1877), right G1, 200um, 200um, 1mm (UF 33095); C – *Cyclodius granulosus* De Man, 1888, right G1, 200um, 200um, 1mm (UF 3017); D – *Cyclodius nitidus* (Dana, 1852) form 1, right G1, 200um, 200um, 2mm (USNM 23141).

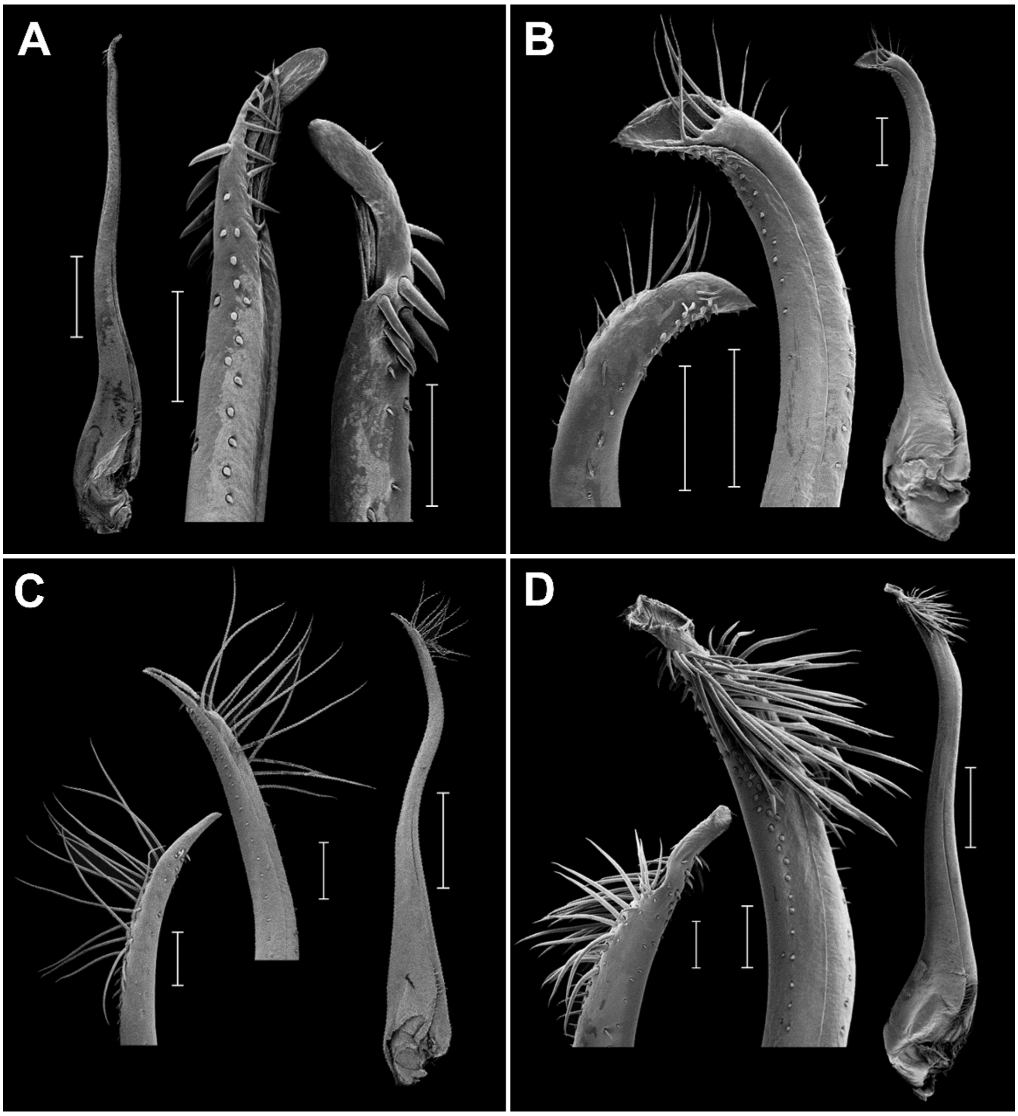


Plate 41. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Cyclodius obscurus* (Hombron & Jacquinot, 1846), right G1, 1mm, 200um, 200um (UF 81387); B – *Cyclodius paumotensis* (Rathbun, 1907), right G1, 200um, 200um, 200um (UF 15600); C – *Cyclodius nitidus* (Dana, 1852) form 2, right G1, 200um, 200um, 1mm (UF 3302); D – *Cyclodius ungulatus* (H. Milne Edwards, 1834) right G1, 200um, 200um, 1mm (UF 25663).

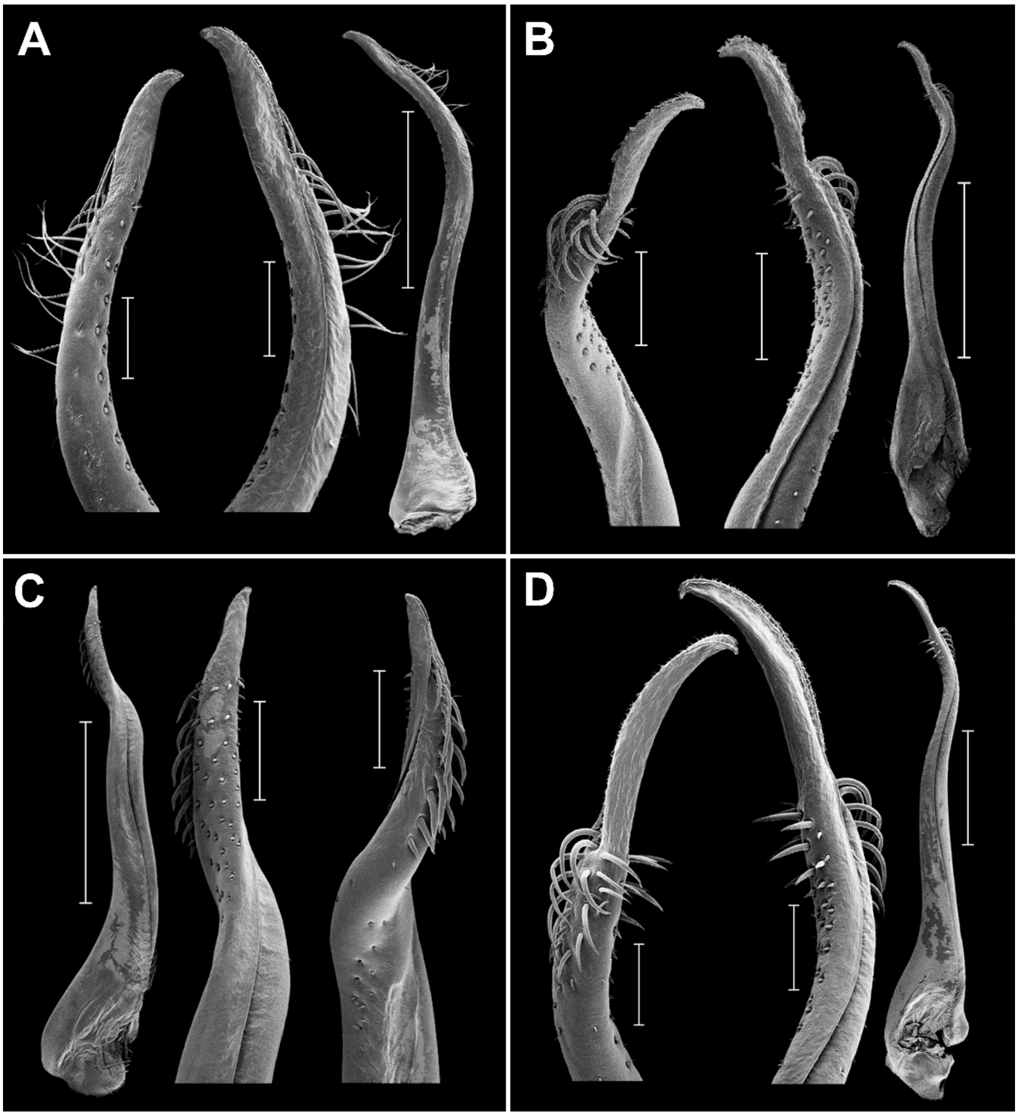


Plate 42. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Luniella pubescens* (Dana, 1852), right G1, 200um, 200um, 1mm (UF 24669); B – *Luniella pugil* (Dana, 1852), right G1, 200um, 200um, 1mm (UF 114804); C – *Luniella scabricula* (Dana, 1852), right G1, 1mm, 200um, 200um (UF 1614); D – *Luniella spinipes* (Heller, 1861), right G1, 200um, 200um, 1mm (UF 14361).

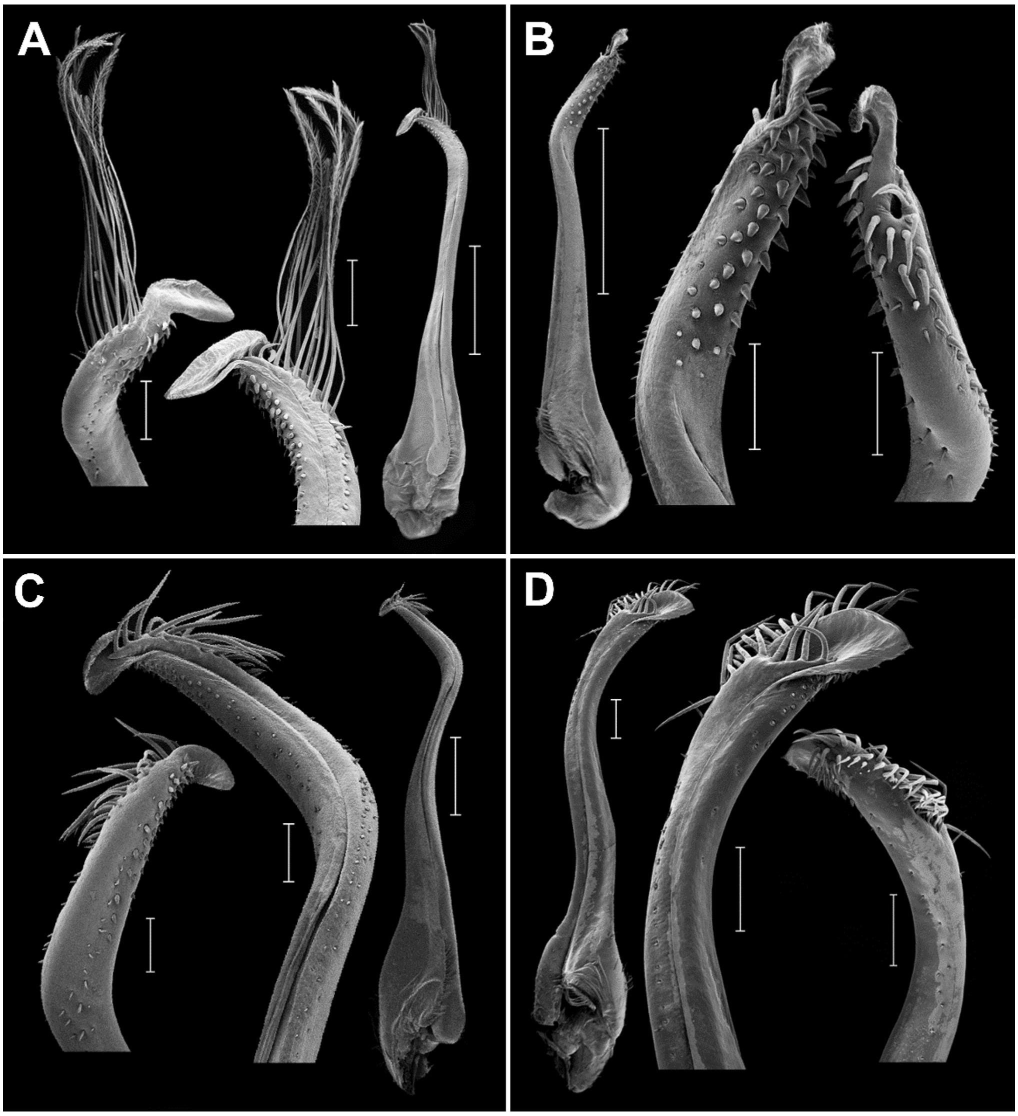


Plate 43. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Pilodius areolatus* (H. Milne Edwards, 1834), right G1, 200um, 200um, 1mm (UF 12807); B – *Pilodius granulatus* Stimpson, 1859, left G1, 1mm, 200um, 200um (UF 17011); C – *Pilodius maotieni* Serène, 1971, right G1, 200um, 200um, 1mm (UF 2631); D – *Pilodius miersi* (Ward, 1936), left G1, 200um, 200um, 200um (UF 25804).

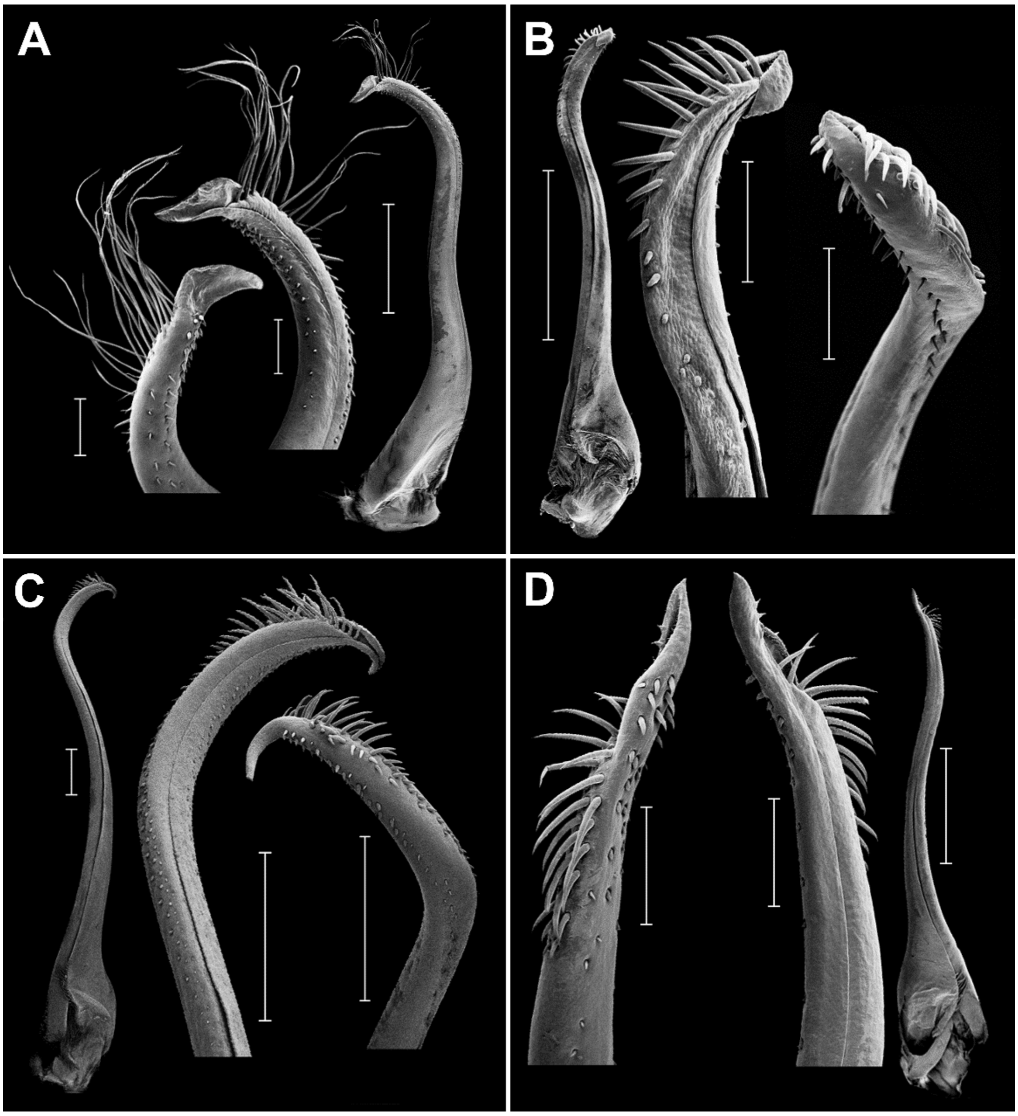


Plate 44. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – *Pilodius moranti* Clark & Galil, 1993, right G1, 200um, 200um, 1mm (QM 15456); B – *Pilodius nigrocrinitus* Stimpson, 1859, left G1, 1mm, 200um, 200um (UF 17075); C – *Pilodius pilumnoides* (White, 1848), left G1, 1mm, 1mm, 1mm (ZRC 1989.3430); D – *Soliella flava* (Rathbun, 1894), right G1, 200um, 200um, 1mm (UF 12254).

Plate 45. First male gonopods of chlorodielline species: internal detail, external detail, and external full. Scale bar measurements presented left to right: *Soliella melanospinis* (Rathbun, 1911), right G1, 200um, 200um, 1mm (ZRC 2013.1647).

Plate 46. Distribution of: A) *Chlorodiella barbata* (Borradaile, 1900); B) *Chlorodiella cochlearis* (Zehntner 1894); C) *Chlorodiella cytherea* (Dana, 1852); and D) *Chlorodiella planapexa* sp. nov. Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

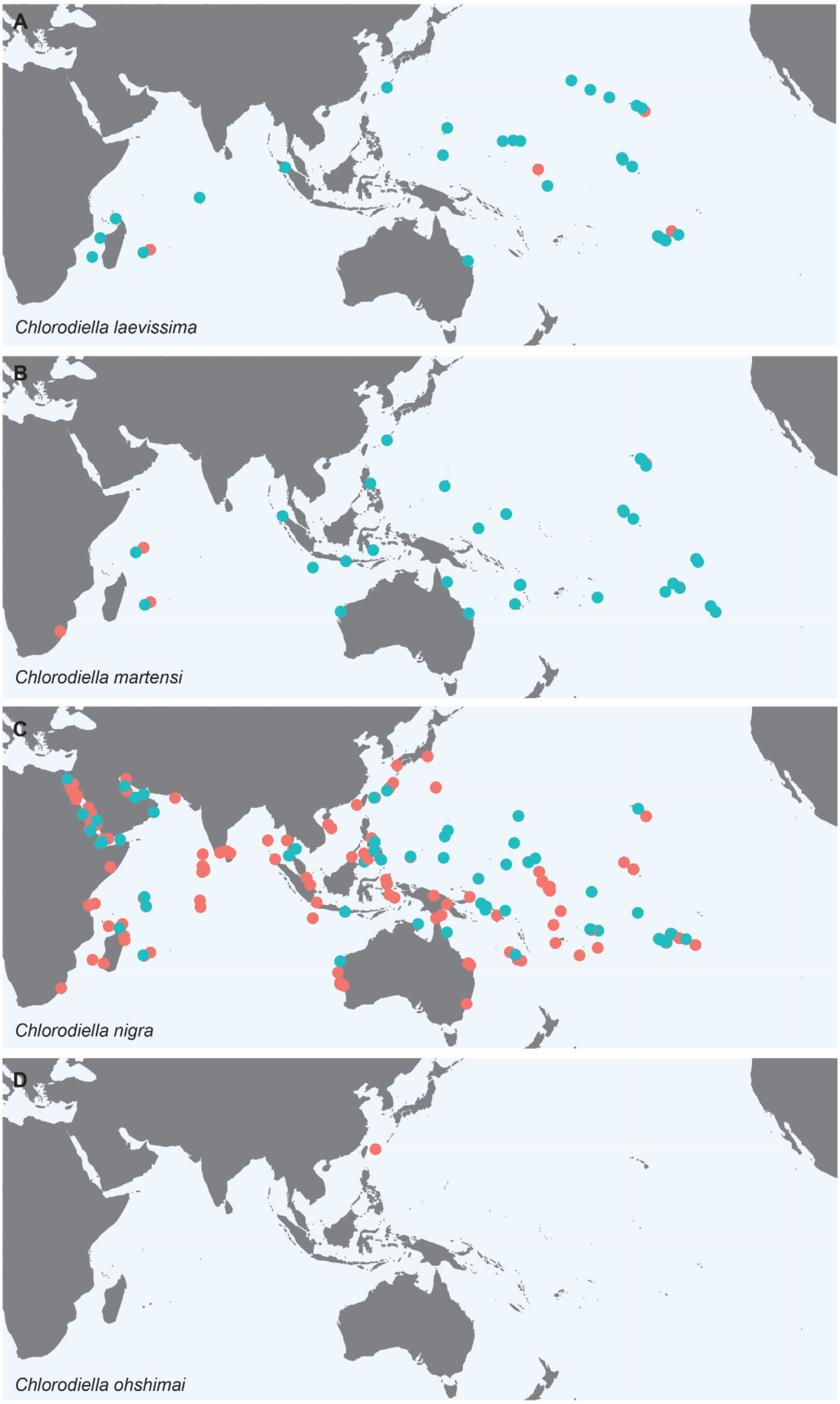


Plate 47. Distribution of: A) *Chlorodiella laevissima* (Dana, 1852); B) *Chlorodiella martensi* (Krauss, 1843); C) *Chlorodiella nigra* (Forskål, 1775); and D) *Chlorodiella ohshimai* Miyake & Takeda, 1967. Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

Plate 48. Distribution of: A) *Chlorodiella quadrilobata* Dai, Cai & Yang, 1996; B) *Chlorodiella xishaensis* Chen & Lan, 1978; C) *Cyclodius drachi* Guinot, 1964; and D) *Cyclodius granulatus* (Targioni-Tozzetti, 1877). Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

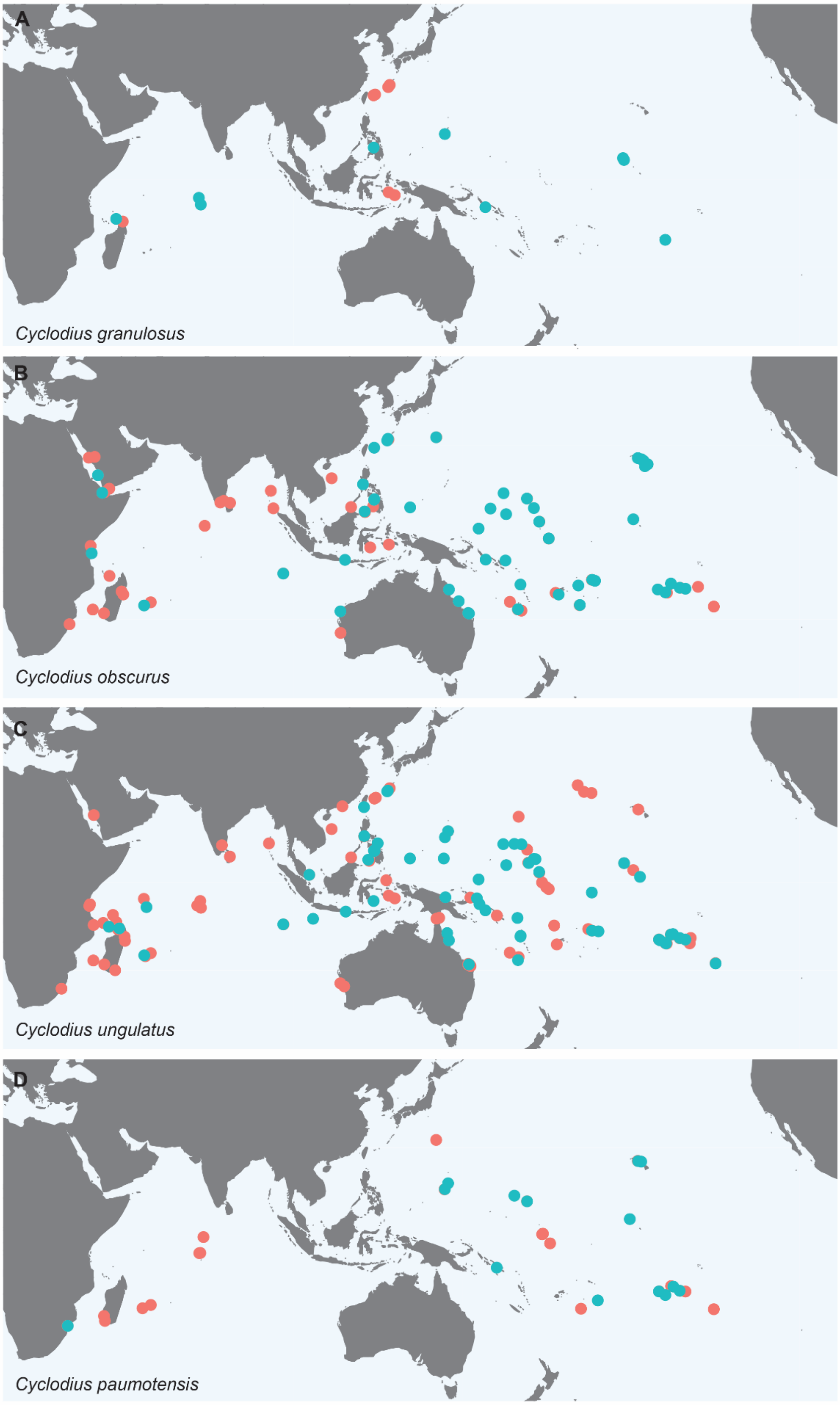


Plate 49. Distribution of: A) *Cyclodius granulosus* De Man, 1888; B) *Cyclodius obscurus* (Hombron & Jacquinot, 1846); C) *Cyclodius ungulatus* (H. Milne Edwards, 1834); and D) *Cyclodius paumotensis* (Rathbun, 1907). Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

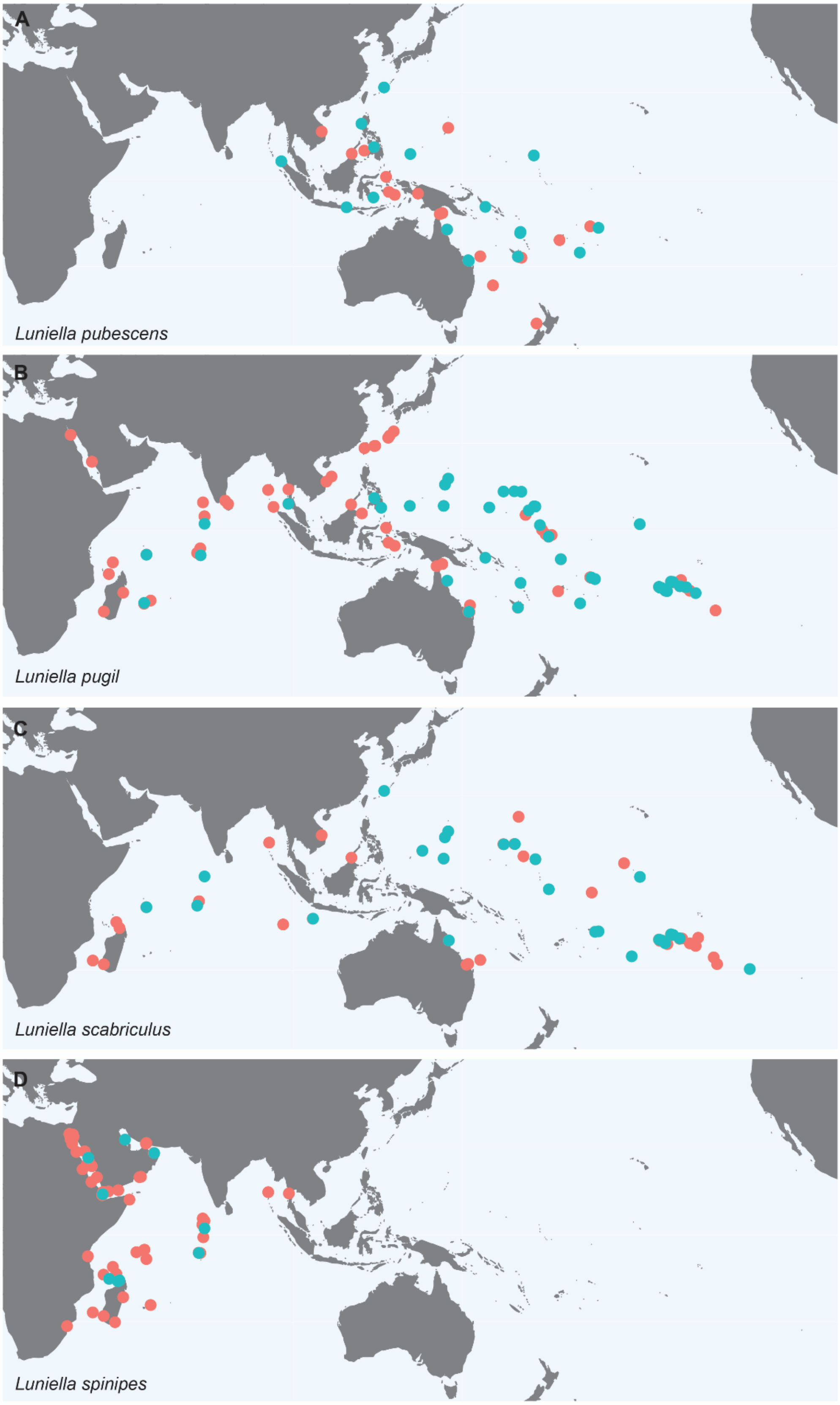


Plate 50. Distribution of: A) *Luniella pubescens* (Dana, 1852); B) *Luniella pugil* (Dana, 1852); C) *Luniella scabriculus* (Dana, 1852); and D) *Luniella spinipes* (Heller, 1861). Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

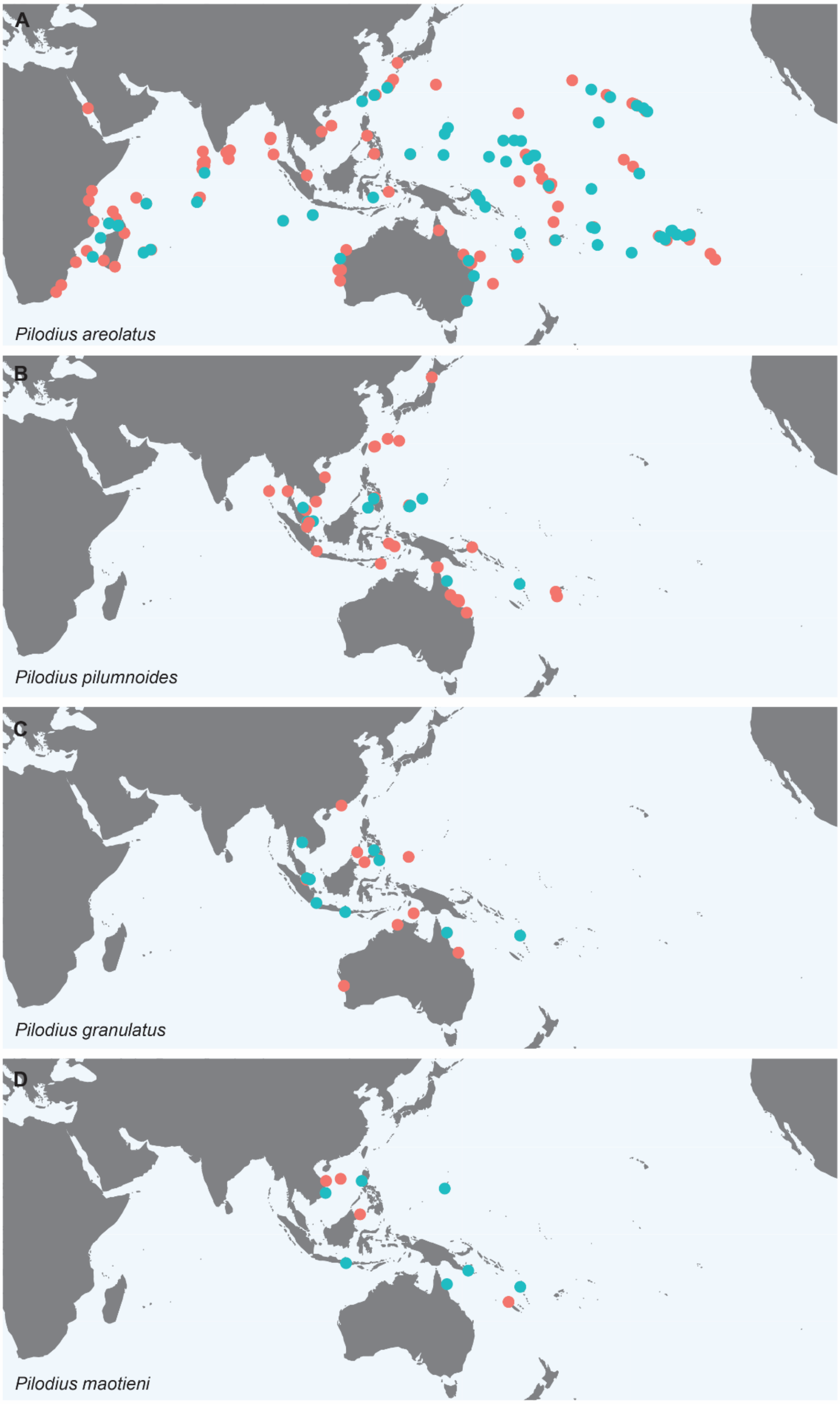


Plate 51. Distribution of: A) *Pilodius areolatus* (H. Milne Edwards, 1834); B) *Pilodius pilumnoides* (White, 1848); C) *Pilodius granulatus* Stimpson, 1858; and D) *Pilodius maotieni* Serène, 1971. Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

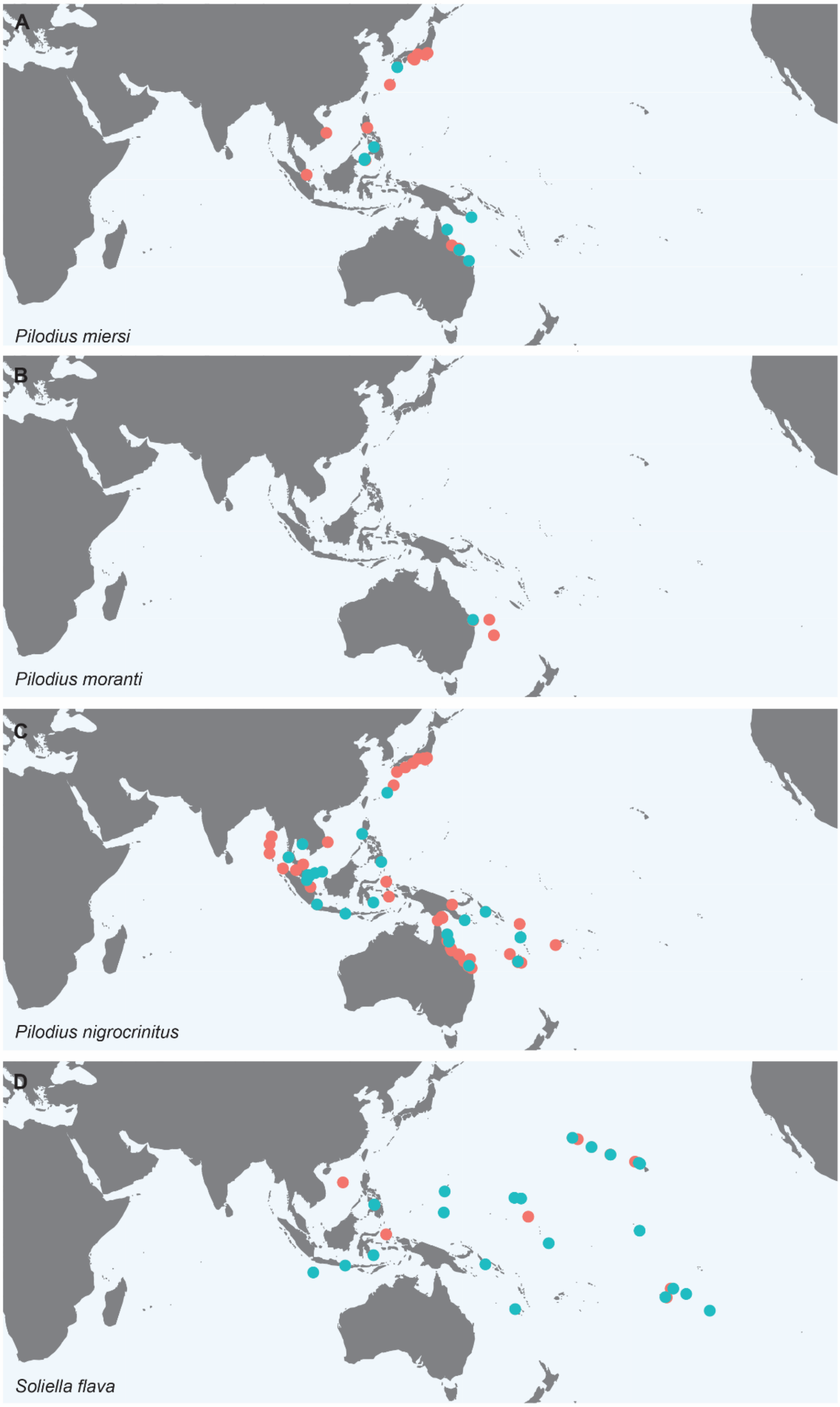


Plate 52. Distribution of: A) *Pilodius miersi* (Ward, 1936); B) *Pilodius moranti* Clark & Galil, 1993; C) *Pilodius nigrocrinitus* Stimpson, 1859; and D) *Soliella flava* (Rathbun, 1894). Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

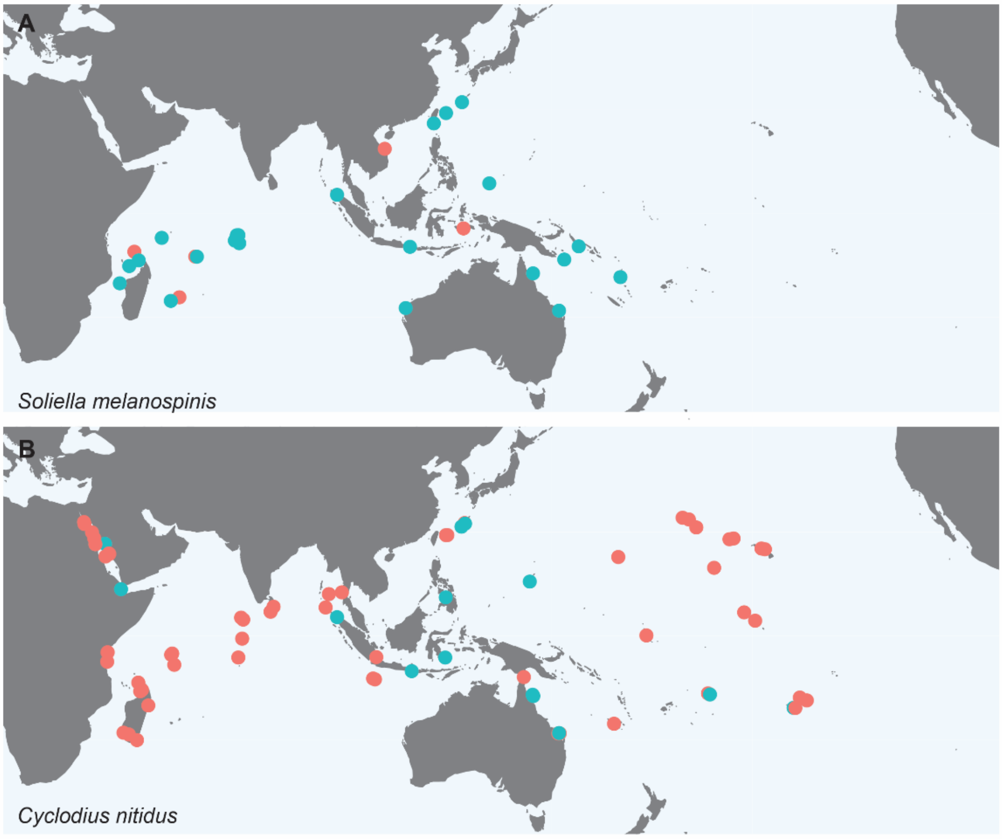


Plate 53. Distribution of: A) *Soliella melanospinis* (Rathbun, 1911), and B) *Cyclodius nitidus*. Localities of specimens examined for this study are indicated with blue dots. Additional localities from the literature are indicated with red dots.

APPENDIX

Publications Produced During Course of Phd

On Xanthidae

Lasley, R. M. Jr, Klaus, S., & Ng, P. K. L., (2015). Phylogenetic relatioships of the Chlorodiellinae with the description of two new genera. *Zoologica Scripta* (submitted).

Lasley, R.M. Jr, Lai, J.C.Y, & Thoma, B.P., (2013). A new genus for *Chlorodiella longimana* (H. Milne Edwards, 1834) supported by morphology and molecular data, with a preliminary phylogeny of the Chlorodiellinae (Crustacea: Decapoda: Xanthidae). *Invertebrate Systematics* 27: 379–390.

Lasley, R.M. Jr, & Ng, P.K.L, (2013). A new species of *Zozymodes* (Crustacea: Decapoda: Xanthidae) from Guam. *Micronesica* 2013-03.

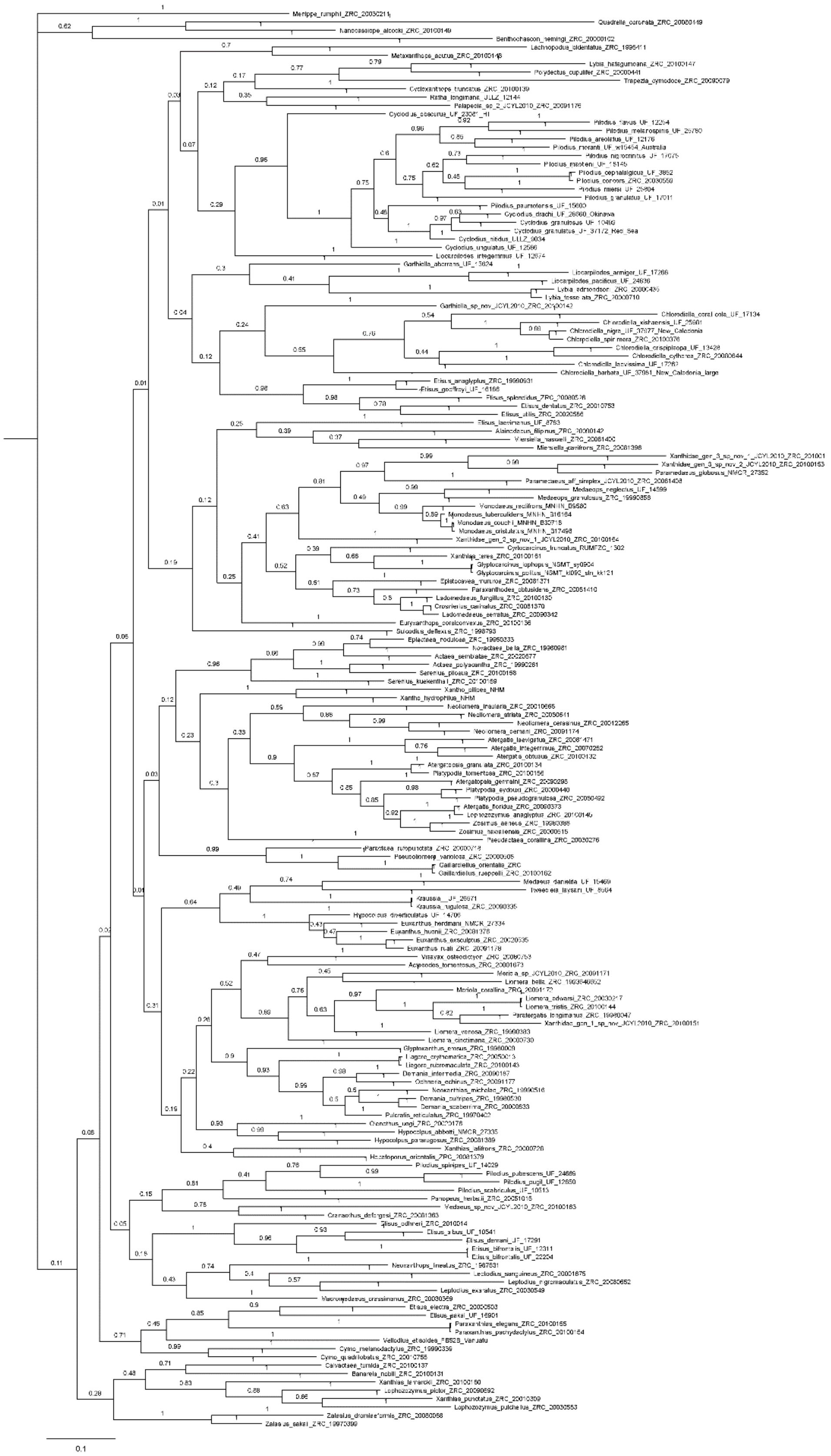
Lasley, R.M. Jr., Mendoza, J.C.E., & Ng, P. K. L., (2010). Two new species of *Guitonia* Garth & Iliffe, 1992 (Crustacea: Decapoda: Brachyura: Xanthidae) from the central and western Pacific Ocean. *Zootaxa* 2684: 1–13.

Others

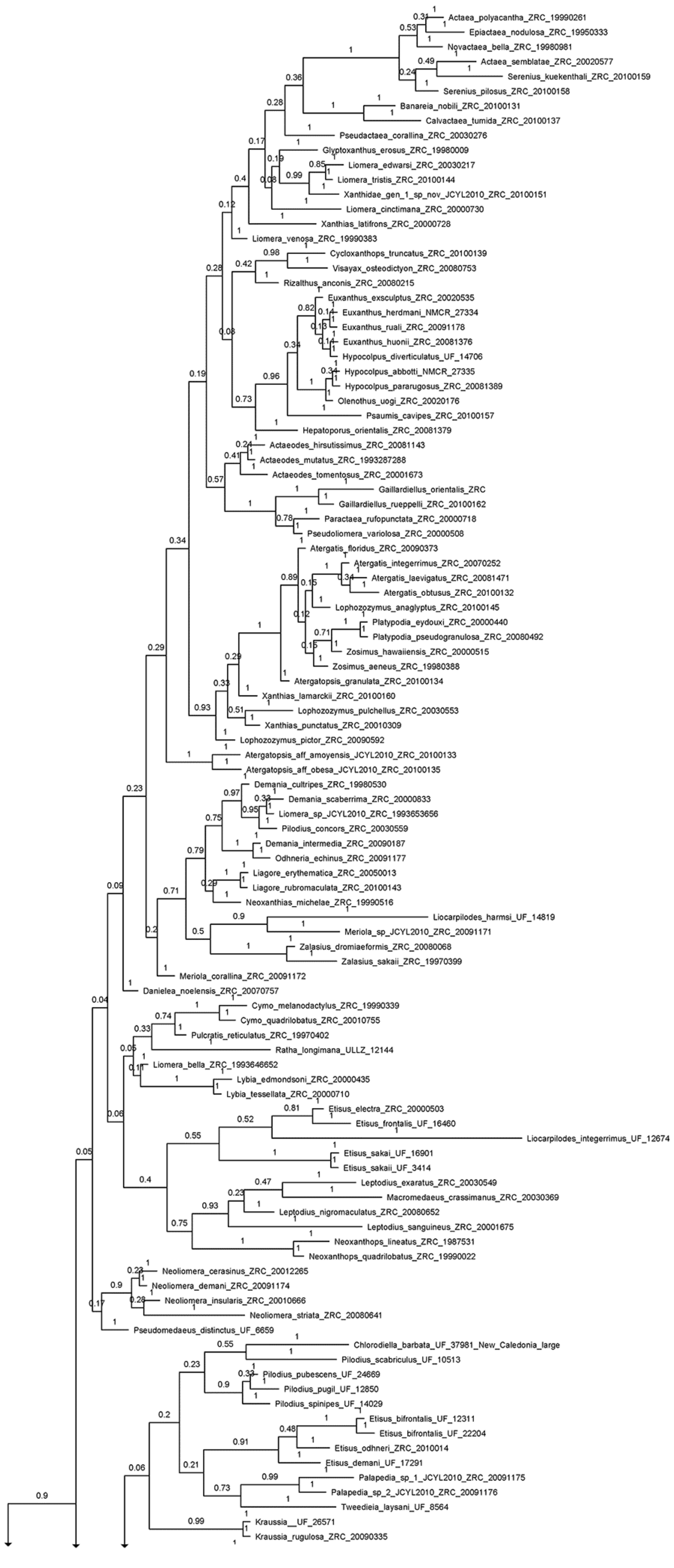
Lasley, R. M. Jr, Jain, A., & Kunte, K., (2013). Alleviating Poverty in India: Biodiversity's Role. *Science* 6148: 840–841.

Dixon, R. & Lasley, R., (2009). Phycology in a shearing shed. *Australian Society for Phycology and Aquatic Botany* 27(2): 3-4.

Supplementary Material



SM 1. COXI BI gene tree


Actaea_polyacantha_ZRC_19990261
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Novactaea_bella_ZRC_19980981
Actaea_semblatae_ZRC_20020577
Serenius_kuekenthali_ZRC_20100159
Serenius_pilosus_ZRC_20100158
Banareia_nobili_ZRC_20100131
Calvactaea_tumida_ZRC_20100137
Pseudactaea_corallina_ZRC_20030276
Glyptoxanthus_erosus_ZRC_19980009
Liomera_edwarsi_ZRC_20030217
Liomera_tristis_ZRC_20100144
Xanthidae_gen_1_sp_nov_JCYL2010_ZRC_20100151
Liomera_cinctimana_ZRC_20000730
Xanthias_latifrons_ZRC_20000728
Liomera_venosa_ZRC_19990383
Cycloxanthops_truncatus_ZRC_20100139
Visayax_osteodictyon_ZRC_20080753
Rizalthus_anconis_ZRC_20080215
Euxanthus_exsculptus_ZRC_20020535
Euxanthus_herdmani_NMCR_27334
Euxanthus_ruali_ZRC_20091178
Euxanthus_huonii_ZRC_20081376
Hypocolpus_diverticulatus_UF_14706
Hypocolpus_abbotti_NMCR_27335
Hypocolpus_pararugosus_ZRC_20081389
Olenothus_uogi_ZRC_20020176
Psaumis_cavipes_ZRC_20100157
Hepatoporus_orientalis_ZRC_20081379
Actaeodes_hirsutissimus_ZRC_20081143
Actaeodes_mutatus_ZRC_1993287288
Actaeodes_tomentosus_ZRC_20001673
Gaillardiellus_orientalis_ZRC
Gaillardiellus_rueppelli_ZRC_20100162
Paractaea_rufopunctata_ZRC_20000718
Pseudoliomera_variolosa_ZRC_20000508
Atergatis_floridus_ZRC_20090373
Atergatis_integerrimus_ZRC_20070252
Atergatis_laevigatus_ZRC_20081471
Atergatis_obtusus_ZRC_20100132
Lophozozymus_anaglyptus_ZRC_20100145
Platypodia_eydouxi_ZRC_20000440
Platypodia_pseudogranulosa_ZRC_20080492
Zosimus_hawaiiensis_ZRC_20000515
Zosimus_aeneus_ZRC_19980388
Atergatopsis_granulata_ZRC_20100134
Xanthias_lamarckii_ZRC_20100160
Lophozozymus_pulchellus_ZRC_20030553
Xanthias_punctatus_ZRC_20010309
Lophozozymus_pictor_ZRC_20090592
Atergatopsis_aff_amoyensis_JCYL2010_ZRC_20100133
Atergatopsis_aff_obesa_JCYL2010_ZRC_20100135
Demania_cultripes_ZRC_19980530
Demania_scaberrima_ZRC_20000833
Liomera_sp_JCYL2010_ZRC_1993653656
Pilodius_concors_ZRC_20030559
Demania_intermedia_ZRC_20090187
Odhneria_echinus_ZRC_20091177
Liagore_erythematica_ZRC_20050013
Liagore_rubromaculata_ZRC_20100143
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Zalasius_sakaii_ZRC_19970399
Meriola_corallina_ZRC_20091172
Danielea_noelensis_ZRC_20070757
Cymo_melanodactylus_ZRC_19990339
Cymo_quadrilobatus_ZRC_20010755
Pulcratis_reticulatus_ZRC_19970402
Ratha_longimana_ULLZ_12144
Liomera_bella_ZRC_1993646652
Lybia_edmondsoni_ZRC_20000435
Lybia_tessellata_ZRC_20000710
Etisus_electra_ZRC_20000503
Etisus_frontalis_UF_16460
Liocarpilodes_integerrimus_UF_12674
Etisus_sakai_UF_16901
Etisus_sakaii_UF_3414
Leptodius_exaratus_ZRC_20030549
Macromedaeus_crassimanus_ZRC_20030369
Leptodius_nigromaculatus_ZRC_20080652
Leptodius_sanguineus_ZRC_20001675
Neoxanthops_lineatus_ZRC_1987531
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Neoliomera_demani_ZRC_20091174
Neoliomera_insularis_ZRC_20010666
Neoliomera_striata_ZRC_20080641
Pseudomedaeus_distinctus_UF_6659
Chlorodiella_barbata_UF_37981_New_Caledonia_large
Pilodius_scabriculus_UF_10513
Pilodius_pubescens_UF_24669
Pilodius_pugil_UF_12850
Pilodius_spinipes_UF_14029
Etisus_bifrontalis_UF_12311
Etisus_bifrontalis_UF_22204
Etisus_odhneri_ZRC_2010014
Etisus_demani_UF_17291
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Palapedia_sp_2_JCYL2010_ZRC_20091176
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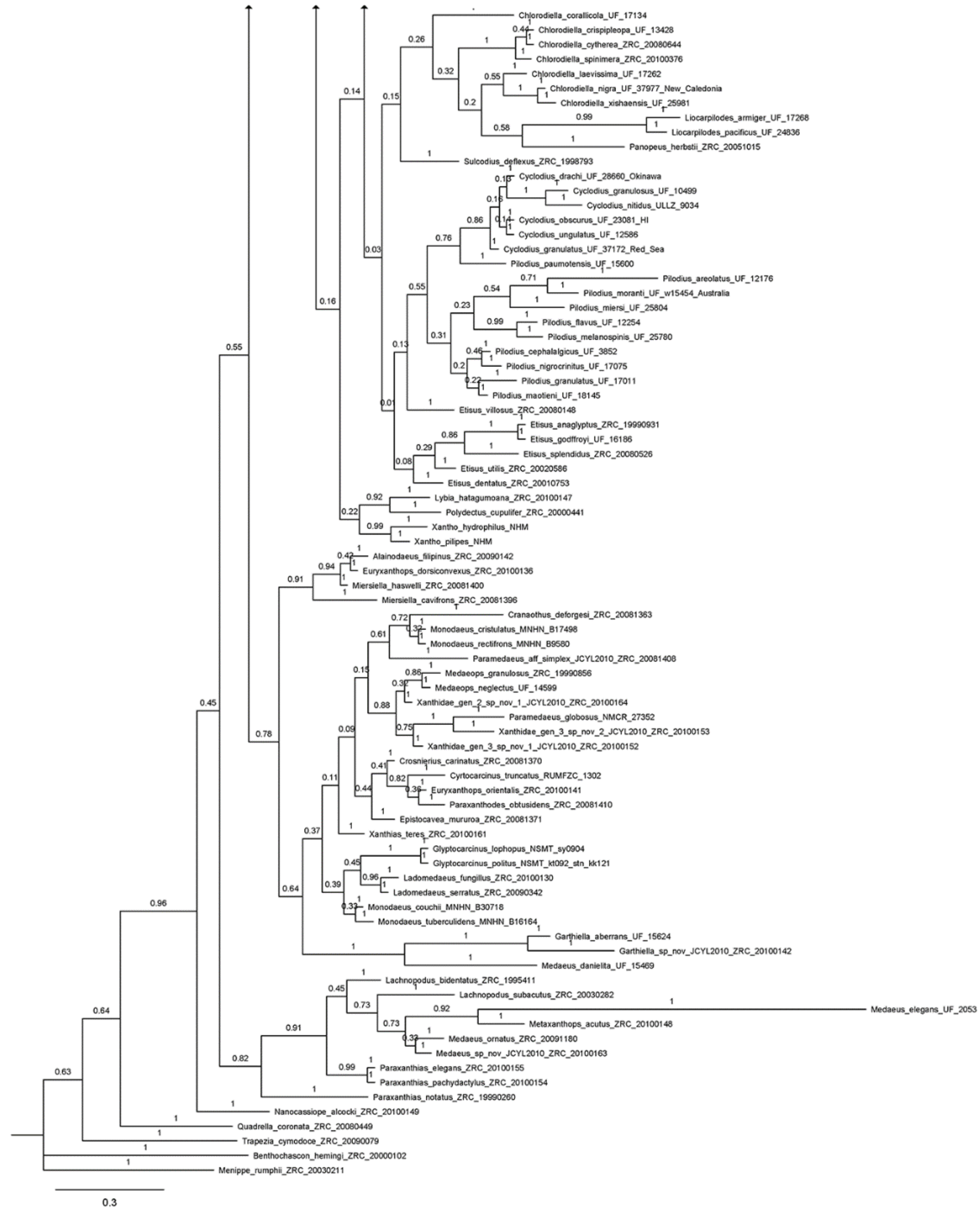
Kraussia__UF_26571
Kraussia_rugulosa_ZRC_20090335



SM 2. H3 BI gene tree

SM 3. H3 ML gene tree

SM 4. List of terminal taxa in COXI phylogeny with locality and catalog number

Taxa	Locality	Catalog number
Chlorodiella barbata	Heron Island, Australia	UF 25970
Chlorodiella barbata	Mo'orea, French Polynesia	NMNH MOO_0372
Chlorodiella barbata	Mo'orea, French Polynesia	NMNH MOO_12890_larva
Chlorodiella barbata	New Caledonia	UF 37981a
Chlorodiella barbata	New Caledonia	UF 37981b
Chlorodiella barbata	Heron Island, Australia	UF 25610
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_DL494
Chlorodiella barbata	Reunion Island	UF 12572
Chlorodiella barbata	Lizard Island, Australia	UF 17105
Chlorodiella barbata	Reunion Island	UF 12597
Chlorodiella barbata	Okinawa, Japan	UF 27004
Chlorodiella barbata	Guam	UF 2881
Chlorodiella barbata	Mo'orea, French Polynesia	UF 9854
Chlorodiella barbata	Reunion Island	UF 12645
Chlorodiella barbata	Guam	UF 2962
Chlorodiella barbata	Mo'orea, French Polynesia	UF 9854
Chlorodiella barbata	Heron Island, Australia	UF 25049
Chlorodiella barbata	Guam	UF 2024
Chlorodiella barbata	Reunion Island	UF 12645
Chlorodiella barbata	Reunion Island	UF 12567
Chlorodiella barbata	Reunion Island	UF 12467
Chlorodiella barbata	Guam	UF 2063
Chlorodiella barbata	Reunion Island	UF 12646
Chlorodiella barbata	Fiji	UF 1740
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0445
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_3434
Chlorodiella barbata	Heron Island, Australia	UF 24998
Chlorodiella barbata	Mo'orea, French Polynesia	UF 10094b
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_034
Chlorodiella barbata	Bali, Indonesia	ZRC rBALI_0005
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0442
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_DL488
Chlorodiella barbata	Reunion Island	UF 12646
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0439
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0431
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_089
Chlorodiella barbata	Mo'orea, French Polynesia	UF 10094
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0446
Chlorodiella barbata	Heron Island, Australia	UF 25049
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_12647_larva
Chlorodiella barbata	Mo'orea, French Polynesia	UF 9855
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_010
Chlorodiella barbata	Reunion Island	UF 12644
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0028
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_DL455B

Chlorodiella barbata	Heron Island, Australia	UF 25244
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_081
Chlorodiella barbata	Fiji	UF 1740
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_12187_Larva
Chlorodiella barbata	Heron Island, Australia	UF 25612
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0437
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_12649_larva
Chlorodiella barbata	Heron Island, Australia	UF 25102
Chlorodiella barbata	Heron Island, Australia	UF 25123
Chlorodiella barbata	Heron Island, Australia	UF 24707
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0491a
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0443
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_065
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0438
Chlorodiella barbata	Heron Island, Australia	UF 24706
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_DL442B
Chlorodiella barbata	Mo'orea, French Polynesia	UF JTX_015
Chlorodiella barbata	Mo'orea, French Polynesia	UF 9855
Chlorodiella barbata	Reunion Island	UF 12572
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0391
Chlorodiella barbata	Reunion Island	UF 12644
Chlorodiella barbata	Mo'orea, French Polynesia	UF 9856
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_JTX_026
Chlorodiella barbata	Reunion Island	UF 12589
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0025
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0444
Chlorodiella barbata	Mo'orea, French Polynesia	UF MOO_0433
Chlorodiella barbata	Guam	UF 2902
Chlorodiella barbata	Reunion Island	UF 12571
Chlorodiella clymene	Solomon Islands	UF 3338
Chlorodiella clymene	Palau	UF 3880
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_3264
Chlorodiella clymene	Ningaloo Reef, Australia	ZRC 2010.0376
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_1868
Chlorodiella clymene	Philippines	ZRC 2013.0565
Chlorodiella clymene	Heron Island, Australia	UF 24753
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2854
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2712
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2640
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2606
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2750
Chlorodiella clymene	Heron Island, Australia	UF 24648
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2598
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2503
Chlorodiella clymene	Lizard Island, Australia	UF 17865
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2808
Chlorodiella clymene	Wake Island	UF 8576

Chlorodiella clymene	Ningaloo Reef, Australia	UF 22116
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2766
Chlorodiella clymene	Mo'orea, French Polynesia	NMNH MOO_11835_larva
Chlorodiella clymene	Guam	UF 2779
Chlorodiella clymene	Bali, Indonesia	NMNH BALI_2762
Chlorodiella clymene	Mo'orea, French Polynesia	UF 10004
Chlorodiella clymene	Mo'orea, French Polynesia	UF MOO_12163_larva
Chlorodiella clymene	Samoa	UF 9533
Chlorodiella clymene	Bali, Indonesia	UF BALI_2608
Chlorodiella clymene	Bali, Indonesia	UF BALI_2361
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1567
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1591
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1131
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1575
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_2180
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1111
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1677
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1234
Chlorodiella cochlearis	Bali, Indonesia	NMNH BALI_1219
Chlorodiella cochlearis	Lizard Island, Australia	UF 17134
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL359Z
Chlorodiella cytherea	Tuamotu Islands	UF 1660
Chlorodiella cytherea	Cook Islands	UF 11711
Chlorodiella cytherea	Cook Islands	UF 11717
Chlorodiella cytherea	Tuamotu Islands	UF 1665
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 10000
Chlorodiella cytherea	Cook Islands	UF 13221
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL507
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 9853b
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL454Z
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_0468
Chlorodiella cytherea	Cook Islands	UF 1360
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 1607
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 24262
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_0471
Chlorodiella cytherea	Cook Islands	UF 11713
Chlorodiella cytherea	Cook Islands	UF 11715
Chlorodiella cytherea	Great Barrier Reef	UF QL_6
Chlorodiella cytherea	Hawaiian Islands	UF 8763
Chlorodiella cytherea	Hawaiian Islands	UF 12341
Chlorodiella cytherea	Hawaiian Islands	UF 12332
Chlorodiella cytherea	Hawaiian Islands	UF 12144
Chlorodiella cytherea	Line Islands	UF 3783
Chlorodiella cytherea	Hawaiian Islands	UF 8737
Chlorodiella cytherea	Hawaiian Islands	UF 12145
Chlorodiella cytherea	Christmas Island	ZRC 2010.0373
Chlorodiella cytherea	Japan	UF 7211

Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL235B
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 15923
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL359X
Chlorodiella cytherea	Vanuatu	ZRC VM54
Chlorodiella cytherea	Majuro	UF 13428
Chlorodiella cytherea	Guam	UF 4013
Chlorodiella cytherea	Marshall Island	UF 13428
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL214
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 9697b
Chlorodiella cytherea	Tuamotu Islands	UF 1676
Chlorodiella cytherea	Mo'orea, French Polynesia	UF 9852
Chlorodiella cytherea	Wake Island	UF 36087
Chlorodiella cytherea	Mo'orea, French Polynesia	UF MOO_DL359Y
Chlorodiella davaoensis	Aceh, Indonesia	NMNH ACEH_1820
Chlorodiella davaoensis	Aceh, Indonesia	NMNH ACEH_2011
Chlorodiella davaoensis	Lizard Island, Australia	UF 17094
Chlorodiella davaoensis	Heron Island, Australia	UF 25986
Chlorodiella davaoensis	Heron Island, Australia	UF 25523
Chlorodiella davaoensis	Xisha Islands	IOCAS XXXX708
Chlorodiella davaoensis	Heron Island, Australia	UF 24891
Chlorodiella davaoensis	Ningaloo Reef, Australia	ZRC NING_0033
Chlorodiella davaoensis	Madagascar	UF 14355
Chlorodiella davaoensis	Heron Island, Australia	UF 25552
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22620
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 21429
Chlorodiella davaoensis	Heron Island, Australia	UF 25450
Chlorodiella davaoensis	Heron Island, Australia	UF 24914
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 21426
Chlorodiella davaoensis	Heron Island, Australia	UF 25920
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22470
Chlorodiella davaoensis	Heron Island, Australia	UF 25554
Chlorodiella davaoensis	Heron Island, Australia	UF 25548
Chlorodiella davaoensis	Heron Island, Australia	UF 24965
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22475
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 21815
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22472
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 21516
Chlorodiella davaoensis	Heron Island, Australia	UF 25546
Chlorodiella davaoensis	Panglao, Philippines	ZRC 2008.0644
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22616
Chlorodiella davaoensis	Heron Island, Australia	UF 25444
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22617
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22479
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22164
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22473
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 21519
Chlorodiella davaoensis	Ningaloo Reef, Australia	UF 22618

Chlorodiella davaoensis	Heron Island, Australia	UF 24791
Chlorodiella laevissima	Line Islands	UF 11071
Chlorodiella laevissima	Line Islands	UF 10562
Chlorodiella laevissima	Line Islands	UF 10566b
Chlorodiella laevissima	Line Islands	UF 11070b
Chlorodiella laevissima	Line Islands	UF 11174b
Chlorodiella laevissima	Line Islands	UF 11179b
Chlorodiella laevissima	Line Islands	UF 11041
Chlorodiella laevissima	Line Islands	UF 10563b
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1222
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1832
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_2458
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1246
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_2464
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1234
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_2457
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1129
Chlorodiella laevissima	Scattered Islands	UF 21117
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_11089_larva
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9851
Chlorodiella laevissima	Heron Island, Australia	UF 24810
Chlorodiella laevissima	Reunion Island	UF 13085
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_11085_larva
Chlorodiella laevissima	Heron Island, Australia	UF 24870
Chlorodiella laevissima	Oahu	UF 17927
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 23798
Chlorodiella laevissima	Okinawa, Japan	UF 28664
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9851
Chlorodiella laevissima	Heron Island, Australia	UF 24804
Chlorodiella laevissima	Reunion Island	UF 13085
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9850
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_m634
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_m809
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 13851
Chlorodiella laevissima	Line Islands	UF dLIN_1105
Chlorodiella laevissima	Line Islands	UF dLIN_1103
Chlorodiella laevissima	Line Islands	UF 13803
Chlorodiella laevissima	Line Islands	UF 11646
Chlorodiella laevissima	Line Islands	UF 10563
Chlorodiella laevissima	Line Islands	UF dLIN_11001
Chlorodiella laevissima	Reunion Island	UF 13055
Chlorodiella laevissima	Scattered Islands	UF 21089A
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1380
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1245
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1237
Chlorodiella laevissima	Scattered Islands	UF 20739
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1305

Chlorodiella laevissima	Reunion Island	UF 13094
Chlorodiella laevissima	Reunion Island	UF 12675
Chlorodiella laevissima	Aceh, Indonesia	NMNH ACEH_1849
Chlorodiella laevissima	Hawaiian Islands	UF 12211
Chlorodiella laevissima	Hawaiian Islands	UF 12328
Chlorodiella laevissima	Hawaiian Islands	UF 12007
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_m4771
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 13843
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9632
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_11526_larva
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 13843
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9838
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_3931
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_m400
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_12997_larva
Chlorodiella laevissima	Mo'orea, French Polynesia	UF 9838b
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_12344_larva
Chlorodiella laevissima	Mo'orea, French Polynesia	UF MOO_12455_larva
Chlorodiella marcusi	Red Sea	UF 33020
Chlorodiella marcusi	Djibouti	UF 33090
Chlorodiella marcusi	Red Sea	UF 37295
Chlorodiella marcusi	Red Sea	UF 33007
Chlorodiella marcusi	Red Sea	UF 36830
Chlorodiella martensi	Aceh, Indonesia	NMNH ACEH_1562
Chlorodiella martensi	Aceh, Indonesia	NMNH ACEH_2406
Chlorodiella martensi	Aceh, Indonesia	NMNH ACEH_1568
Chlorodiella martensi	Aceh, Indonesia	NMNH ACEH_1554
Chlorodiella martensi	Aceh, Indonesia	NMNH ACEH_2378
Chlorodiella martensi	Heron Island, Australia	NMNH 24995
Chlorodiella martensi	Okinawa, Japan	UF 7176
Chlorodiella martensi	Sulawesi, Indonesia	ZRC 2013.1572
Chlorodiella martensi	Reunion Island	UF 13023
Chlorodiella martensi	Reunion Island	UF 12861
Chlorodiella martensi	Aceh, Indonesia	UF ACEH_1227
Chlorodiella martensi	Mo'orea, French Polynesia	UF 10066b
Chlorodiella martensi	Tuamotu Islands	UF 1627
Chlorodiella martensi	Mo'orea, French Polynesia	UF 10065
Chlorodiella martensi	Marquesas	UF 30027
Chlorodiella martensi	Mo'orea, French Polynesia	UF 9626
Chlorodiella martensi	Guam	UF f/1256a
Chlorodiella martensi	Line Islands	UF 11190
Chlorodiella martensi	Mo'orea, French Polynesia	UF MOO_12581_larva
Chlorodiella martensi	Line Islands	UF 9757b
Chlorodiella martensi	Line Islands	UF 11648
Chlorodiella martensi	Mo'orea, French Polynesia	UF 9966b
Chlorodiella martensi	Line Islands	UF 11066
Chlorodiella martensi	Mo'orea, French Polynesia	UF 9966

Chlorodiella martensi	Mo'orea, French Polynesia	UF 9759
Chlorodiella martensi	Mo'orea, French Polynesia	UF 15632
Chlorodiella martensi	Mo'orea, French Polynesia	UF m593
Chlorodiella martensi	Line Islands	UF 11107
Chlorodiella martensi	Mo'orea, French Polynesia	UF 9633
Chlorodiella martensi	Tuamotu Islands	UF 9637
Chlorodiella martensi	Mo'orea, French Polynesia	UF 15635
Chlorodiella martensi	New Caledonia	UF 37969
Chlorodiella martensi	Heron Island, Australia	UF 24745
Chlorodiella martensi	Lizard Island, Australia	UF 17836
Chlorodiella martensi	Ningaloo Reef, Australia	UF 21545
Chlorodiella martensi	Heron Island, Australia	UF 24745
Chlorodiella martensi	Lizard Island, Australia	UF 17836
Chlorodiella martensi	New Caledonia	UF 37971
Chlorodiella martensi	Heron Island, Australia	UF 25519
Chlorodiella martensi	Heron Island, Australia	UF 24655
Chlorodiella martensi	Heron Island, Australia	UF 24916
Chlorodiella nigra	Red Sea	UF 36711
Chlorodiella nigra	Red Sea	UF 36712
Chlorodiella nigra	Okinawa, Japan	UF 36996
Chlorodiella nigra	Reunion Island	UF 12650
Chlorodiella nigra	Madagascar	UF 14606
Chlorodiella nigra	Madagascar	UF 14527
Chlorodiella nigra	Madagascar	UF 14288
Chlorodiella nigra	Madagascar	UF 14275
Chlorodiella nigra	Oman	UF 17948
Chlorodiella nigra	New Caledonia	UF 37977
Chlorodiella nigra	Solomon Islands	UF 3320
Chlorodiella nigra	Bali, Indonesia	ZRC rBALI_0206
Chlorodiella nigra	Okinawa, Japan	UF 26946
Chlorodiella pauli	Samoa	UF 9544c
Chlorodiella pauli	Samoa	UF 9544b
Chlorodiella pauli	Guam	UF 1304
Chlorodiella pauli	New Caledonia	UF 37973
Chlorodiella pauli	Samoa	UF 9544a
Chlorodiella pauli	Guam	UF 1256
Chlorodiella pauli	Guam	UF 2804
Chlorodiella pauli	Guam	UF 2024
Chlorodiella pauli	Guam	UF 2922
Chlorodiella pauli	Guam	UF 1990
Chlorodiella pauli	Guam	UF 2061
Chlorodiella pauli	Guam	UF 2912
Chlorodiella pauli	Guam	UF 391
Chlorodiella pauli	Guam	UF 1979
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1885
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1201
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1075

Chlorodiella soni	Bali, Indonesia	NMNH BALI_2774
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1069
Chlorodiella soni	Scattered Islands	UF 20514
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2286
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1997
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2464
Chlorodiella soni	Scattered Islands	UF 20534a
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2298
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2296
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1179
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2465
Chlorodiella soni	Scattered Islands	UF 20744B
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2264
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2957
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1264
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1261
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2713
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1444
Chlorodiella soni	Scattered Islands	UF 20534a
Chlorodiella soni	Mayotte	UF 13611
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2689
Chlorodiella soni	Madagascar	UF 16576a
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1809
Chlorodiella soni	Madagascar	UF 14295
Chlorodiella soni	Mayotte	UF 13627
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2940
Chlorodiella soni	Madagascar	UF 16576a
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2036
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1190
Chlorodiella soni	Scattered Islands	UF 20514a
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2548
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2571
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_1426
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2447
Chlorodiella soni	Aceh, Indonesia	NMNH ACEH_2256
Chlorodiella soni	Okinawa, Japan	UF 28657
Chlorodiella soni	Heron Island, Australia	UF 25608
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2204
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1385
Chlorodiella soni	Heron Island, Australia	UF 25556
Chlorodiella soni	Heron Island, Australia	UF 26296
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2769
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1867
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1674
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1513
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1432
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2179

Chlorodiella soni	Bali, Indonesia	NMNH BALI_2450
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2924
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1665
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2725
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1873
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2454
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1861
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1846
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1845
Chlorodiella soni	Ningaloo Reef, Australia	UF 21489
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1845_2
Chlorodiella soni	Lizard Island, Australia	UF 17262
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2824
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1688
Chlorodiella soni	Lizard Island, Australia	UF 17545a
Chlorodiella soni	Ningaloo Reef, Australia	UF 21427
Chlorodiella soni	Sulawesi, Indonesia	ZRC rBALI_0256
Chlorodiella soni	Bali, Indonesia	NMNH BALI_3138
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2763
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2518
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1714
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1227
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1555
Chlorodiella soni	Ningaloo Reef, Australia	UF 21688A
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2183
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2831
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2388
Chlorodiella soni	Lizard Island, Australia	UF 17262
Chlorodiella soni	Ningaloo Reef, Australia	UF 21645
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1685
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2379
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2378
Chlorodiella soni	Heron Island, Australia	UF 25234
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2851
Chlorodiella soni	Heron Island, Australia	UF 25127
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1678
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1259
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1189
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1971
Chlorodiella soni	Ningaloo Reef, Australia	UF 21497
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2225
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1882
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1174
Chlorodiella soni	Ningaloo Reef, Australia	UF 21643
Chlorodiella soni	Bali, Indonesia	NMNH BALI_3086
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2355
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1662

Chlorodiella soni	Bali, Indonesia	NMNH BALI_2825
Chlorodiella soni	Sulawesi, Indonesia	ZRC rBALI_0256
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2764
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1504
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1870
Chlorodiella soni	Ningaloo Reef, Australia	UF 21487
Chlorodiella soni	Ningaloo Reef, Australia	UF 21423
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1424
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2371
Chlorodiella soni	Ningaloo Reef, Australia	ZRC 2010.0381
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1848
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1214
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1236
Chlorodiella soni	Bali, Indonesia	NMNH BALI_1292
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2554
Chlorodiella soni	Heron Island, Australia	UF 25553
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2863
Chlorodiella soni	Bali, Indonesia	NMNH BALI_2894
Chlorodiella sp	Bali, Indonesia	NMNH BALI_1528
Chlorodiella sp	Bali, Indonesia	ZRC 2013.1699
Chlorodiella sp	Bali, Indonesia	NMNH BALI_1651
Chlorodiella xishaensis	Panglao, Philippines	ZRC 2010.0289
Chlorodiella xishaensis	Bali, Indonesia	NMNH BALI_2186
Chlorodiella xishaensis	Bali, Indonesia	NMNH BALI_2181
Chlorodiella xishaensis	New Caledonia	UF 37970a
Chlorodiella xishaensis	New Caledonia	UF 37974
Chlorodiella xishaensis	Heron Island, Australia	UF 24670
Chlorodiella xishaensis	Okinawa, Japan	UF 26903
Chlorodiella xishaensis	Heron Island, Australia	UF 24678
Chlorodiella xishaensis	Bali, Indonesia	UF BALI_2361
Chlorodiella xishaensis	Heron Island, Australia	UF 24680
Chlorodiella xishaensis	Heron Island, Australia	UF 24658
Chlorodiella xishaensis	Heron Island, Australia	UF 24657
Chlorodiella xishaensis	Heron Island, Australia	UF 24999
Chlorodiella xishaensis	Heron Island, Australia	UF 24827
Chlorodiella xishaensis	Heron Island, Australia	UF 25566
Chlorodiella xishaensis	Heron Island, Australia	UF 24948
Chlorodiella xishaensis	Heron Island, Australia	UF 24740
Chlorodiella xishaensis	Heron Island, Australia	UF 24778
Chlorodiella xishaensis	Heron Island, Australia	UF 25981
Chlorodiella xishaensis	Heron Island, Australia	UF 24872
Chlorodiella xishaensis	Heron Island, Australia	UF 24668
Chlorodiella xishaensis	Heron Island, Australia	UF 25880
Chlorodiella xishaensis	Heron Island, Australia	UF 24659
Chlorodiella xishaensis	Heron Island, Australia	UF 24668
Chlorodiella xishaensis	Bali, Indonesia	NMNH BALI_2361
Chlorodiella xishaensis	Heron Island, Australia	UF 25636

Chlorodiella xishaensis	Heron Island, Australia	UF 24684
Chlorodiella xishaensis	Heron Island, Australia	UF 25981
Chlorodiella xishaensis	Heron Island, Australia	UF 25773
Chlorodiella xishaensis	New Caledonia	UF 37970b
Cyclodius ganulosus	Scattered Islands	UF 21278
Cyclodius ganulosus	Scattered Islands	UF 21190b
Cyclodius ganulosus	Scattered Islands	UF 21190a
Cyclodius ganulosus	Guam	UF 3017
Cyclodius ganulosus	Line Islands	UF 11110
Cyclodius ganulosus	Mo'orea, French Polynesia	UF MOO_0314
Cyclodius ganulosus	Line Islands	UF 11177
Cyclodius ganulosus	Line Islands	UF 10499
Cyclodius ganulosus	Guam	UF 1248
Cyclodius granulatus	Red Sea	UF 37172
Cyclodius granulatus	Djibouti	UF 37892a
Cyclodius granulatus	Djibouti	UF 33095
Cyclodius nitidus	Lizard Island, Australia	UF 16657
Cyclodius nitidus	Lizard Island, Australia	UF 16656
Cyclodius nitidus	Samoan Islands	USNM 23141
Cyclodius nitidus	Lizard Island, Australia	UF 17168
Cyclodius nitidus	Heron Island, Australia	UF 24862
Cyclodius nitidus	Heron Island, Australia	UF 25633
Cyclodius nitidus	Lizard Island, Australia	UF 17175
Cyclodius nitidus	Lizard Island, Australia	UF 16638
Cyclodius nitidus	Heron Island, Australia	UF 25559
Cyclodius nitidus	Heron Island, Australia	UF 24806
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1363
Cyclodius nitidus	Heron Island, Australia	UF 24789
Cyclodius nitidus	Heron Island, Australia	UF 24787
Cyclodius nitidus	Okinawa, Japan	UF 28666
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1249
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1839
Cyclodius nitidus	Heron Island, Australia	UF 24662
Cyclodius nitidus	Panglao, Philippines	ZRC 2008.0642
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1449
Cyclodius nitidus	Heron Island, Australia	UF 24858
Cyclodius nitidus	Heron Island, Australia	UF 24786
Cyclodius nitidus	Great Barrier Reef	UF 17031
Cyclodius nitidus	Okinawa, Japan	UF 28660
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1058
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_2125
Cyclodius nitidus	Samoan Islands	UF 3231
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_2542
Cyclodius nitidus	Bali, Indonesia	ZRC rBALI_0205
Cyclodius nitidus	Heron Island, Australia	UF 24902
Cyclodius nitidus	Heron Island, Australia	UF 24884
Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1450

Cyclodius nitidus	Aceh, Indonesia	NMNH ACEH_1410
Cyclodius nitidus	Heron Island, Australia	UF 24863
Cyclodius nitidus	Sulawesi, Indonesia	ZRC rBALI_0358
Cyclodius obscurus	Hawaiian Islands	UF 8597
Cyclodius obscurus	Hawaiian Islands	UF 8781
Cyclodius obscurus	Hawaiian Islands	UF 23081
Cyclodius obscurus	Red Sea	UF 36780
Cyclodius obscurus	Panglao, Philippines	ZRC 2013.0729
Cyclodius obscurus	Palau	UF 3897
Cyclodius obscurus	Okinawa, Japan	UF 26936
Cyclodius obscurus	Bali, Indonesia	ZRC rBALI_0221
Cyclodius obscurus	Solomon Islands	UF 29676
Cyclodius obscurus	Majuro	UF 2182
Cyclodius obscurus	Okinawa, Japan	UF 26990
Cyclodius obscurus	New Caledonia	UF 17996
Cyclodius obscurus	Mo'orea, French Polynesia	UF MOO_11955_larva
Cyclodius obscurus	Mo'orea, French Polynesia	UF MOO_12173_larva
Cyclodius obscurus	Mo'orea, French Polynesia	UF MOO_11954_larva
Cyclodius obscurus	Tuamotu Islands	UF 18537
Cyclodius obscurus	Tuamotu Islands	UF 18536
Cyclodius obscurus	Mo'orea, French Polynesia	UF MOO_11932_larva
Cyclodius obscurus	New Caledonia	UF 17995
Cyclodius obscurus	Heron Island, Australia	UF 25602
Cyclodius obscurus	Heron Island, Australia	UF 25771
Cyclodius obscurus	Heron Island, Australia	UF 25517
Cyclodius obscurus	Heron Island, Australia	UF 25781
Cyclodius obscurus	Heron Island, Australia	UF 24972
Cyclodius obscurus	Heron Island, Australia	UF 25771
Cyclodius obscurus	Heron Island, Australia	UF 24955
Cyclodius obscurus	Heron Island, Australia	UF 24866
Cyclodius obscurus	Heron Island, Australia	UF 25782
Cyclodius obscurus	Heron Island, Australia	UF 25408
Cyclodius obscurus	Reunion Island	UF 12568
Cyclodius obscurus	Ningaloo Reef, Australia	UF 22101
Cyclodius obscurus	Ningaloo Reef, Australia	ZRC NING_0118
Cyclodius sculptus	Hawaiian Islands	UF 12009
Cyclodius sculptus	French Frigate Shoals	UF 12337
Cyclodius sculptus	Ant Atoll	UF 5277
Cyclodius sculptus	Guam	UF 710
Cyclodius sculptus	Christmas Island	ZRC 2013.163
Cyclodius sculptus	Guam	UF 4074
Cyclodius sculptus	Ningaloo Reef, Australia	UF 22787
Cyclodius sculptus	Red Sea	UF 33026a
Cyclodius sculptus	Djibouti	UF 32927
Cyclodius sculptus	Scattered Islands	UF 20767
Cyclodius sculptus	Mo'orea, French Polynesia	UF 15586
Cyclodius sculptus	Mo'orea, French Polynesia	UF 9808

Cyclodius sculptus	Mo'orea, French Polynesia	UF 15628
Cyclodius sculptus	Mo'orea, French Polynesia	UF 15629
Cyclodius sculptus	Hawaiian Islands	ZRC 2000.0436
Cyclodius sculptus	French Frigate Shoals	UF 12336a
Cyclodius sculptus	Hawaiian Islands	ULLZ 9034
Cyclodius sculptus	French Frigate Shoals	UF 12336b
Cyclodius ungulatus	Taiwan	UF 11802
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1495
Cyclodius ungulatus	Philippines	ZRC 2010.0138
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1976
Cyclodius ungulatus	Heron Island, Australia	UF 25663
Cyclodius ungulatus	Madagascar	UF 14360
Cyclodius ungulatus	Reunion Island	UF 12580
Cyclodius ungulatus	Reunion Island	UF 12560
Cyclodius ungulatus	Reunion Island	UF 12586
Cyclodius ungulatus	Reunion Island	UF BREU_2897
Cyclodius ungulatus	Madagascar	UF 14607
Cyclodius ungulatus	Reunion Island	UF 12559
Cyclodius ungulatus	Reunion Island	UF 12581
Cyclodius ungulatus	Mayotte	UF 13685
Cyclodius ungulatus	Sulawesi, Indonesia	ZRC rBALI_0372
Cyclodius ungulatus	Guam	UF 764
Cyclodius ungulatus	Guam	UF 712
Cyclodius ungulatus	Okinawa, Japan	UF 26796
Cyclodius ungulatus	Guam	UF 4244
Cyclodius ungulatus	Kosrae	UF 14935
Cyclodius ungulatus	Guam	UF 1993
Cyclodius ungulatus	Kosrae	UF 19856
Cyclodius ungulatus	Line Islands	UF 1284
Cyclodius ungulatus	Guam	UF 2999
Cyclodius ungulatus	Reunion Island	UF BREU_2905
Cyclodius ungulatus	Reunion Island	UF BREU_2906
Cyclodius ungulatus	Madagascar	UF 14325
Cyclodius ungulatus	Panglao, Philippines	ZRC 2008.0648a
Cyclodius ungulatus	Heron Island, Australia	UF 25520
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1992
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1858
Cyclodius ungulatus	Mo'orea, French Polynesia	UF 13865
Cyclodius ungulatus	Mo'orea, French Polynesia	UF DL_384B
Cyclodius ungulatus	Samoa	UF 9549
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_12221_larva
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_9847
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_0003
Cyclodius ungulatus	Mo'orea, French Polynesia	UF DL_213
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_0367
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_DL542
Cyclodius ungulatus	Mo'orea, French Polynesia	UF 13866

Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_0002
Cyclodius ungulatus	Mo'orea, French Polynesia	UF 9831
Cyclodius ungulatus	Mo'orea, French Polynesia	UF MOO_m991
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1370
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_1138
Cyclodius ungulatus	Vanuatu	ZRC 2013.1674
Cyclodius ungulatus	Solomon Islands	UF 3326
Cyclodius ungulatus	Heron Island, Australia	UF 25662
Cyclodius ungulatus	Heron Island, Australia	UF 25131
Cyclodius ungulatus	New Caledonia	UF 17998
Cyclodius ungulatus	Bali, Indonesia	NMNH BALI_2190
Cyclodius ungulatus	Heron Island, Australia	UF 25478
Cyclodius ungulatus	Lizard Island, Australia	UF 16641
Cyclodius ungulatus	Panglao, Philippines	ZRC 2008.0648a
Cyclodius ungulatus	Okinawa, Japan	UF 26824
Cyclodius ungulatus	Solomon Islands	UF 3360
Cylcodius paumotensis	Mo'orea, French Polynesia	UF 9791
Cylcodius paumotensis	Mo'orea, French Polynesia	UF 9763
Cylcodius paumotensis	Mo'orea, French Polynesia	UF 15600
Pilodius areolatus	French Frigate Shoals	UF 12368
Pilodius areolatus	Hawaiian Islands	ULLZ 9033
Pilodius areolatus	Hawaiian Islands	UF 12176
Pilodius areolatus	Hawaiian Islands	UF 12437
Pilodius areolatus	Heron Island, Australia	UF 25465
Pilodius areolatus	Reunion Island	UF 12579
Pilodius areolatus	Ningaloo Reef, Australia	UF 21402
Pilodius areolatus	Mo'orea, French Polynesia	UF 9843
Pilodius areolatus	Mo'orea, French Polynesia	UF 15957
Pilodius areolatus	Heron Island, Australia	UF 24910
Pilodius areolatus	Heron Island, Australia	UF 24973
Pilodius areolatus	Heron Island, Australia	UF 25245
Pilodius areolatus	Heron Island, Australia	UF 25557
Pilodius areolatus	Scattered Islands	UF 20232
Pilodius areolatus	Heron Island, Australia	UF 25574
Pilodius areolatus	Scattered Islands	UF 20233
Pilodius areolatus	Majuro	UF 13416a
Pilodius areolatus	Ningaloo Reef, Australia	UF 21401
Pilodius areolatus	Ningaloo Reef, Australia	UF 21430
Pilodius areolatus	Heron Island, Australia	UF 25573
Pilodius areolatus	Heron Island, Australia	UF 24893
Pilodius areolatus	Scattered Islands	UF 20231
Pilodius areolatus	Caroline Islands	UF 5271a
Pilodius areolatus	Tuamotu Islands	UF 1613
Pilodius areolatus	Reunion Island	UF 12607
Pilodius areolatus	Bali, Indonesia	ZRC rBALI_0382
Pilodius areolatus	Bali, Indonesia	ZRC rBALI_0234
Pilodius areolatus	Reunion Island	UF 12585

Pilodius areolatus	Kirimati	UF 10592
Pilodius areolatus	Caroline Islands	UF 5271a
Pilodius areolatus	Solomon Islands	UF 3395
Pilodius areolatus	Madagascar	UF 14206
Pilodius areolatus	Majuro	UF 13416a
Pilodius areolatus	Mo'orea, French Polynesia	UF MOO_12786_larva
Pilodius areolatus	Okinawa, Japan	UF 28639
Pilodius areolatus	Okinawa, Japan	UF 26943
Pilodius areolatus	Ningaloo Reef, Australia	UF 21601
Pilodius areolatus	Ningaloo Reef, Australia	UF 21394
Pilodius areolatus	Ningaloo Reef, Australia	UF 22168
Pilodius areolatus	Reunion Island	UF 12807
Pilodius areolatus	Kirimati	UF 10723
Pilodius areolatus	Mo'orea, French Polynesia	UF MOO_12795_larva
Pilodius areolatus	Heron Island, Australia	UF 25576
Pilodius areolatus	Reunion Island	UF 12582
Pilodius areolatus	Mo'orea, French Polynesia	UF MOO_12413_larva
Pilodius areolatus	Cook Islands	UF 10334
Pilodius areolatus	Ningaloo Reef, Australia	UF 21977
Pilodius areolatus	Mo'orea, French Polynesia	UF 10097
Pilodius areolatus	Ningaloo Reef, Australia	UF 21480
Pilodius areolatus	Mo'orea, French Polynesia	UF 10090
Pilodius areolatus	Ningaloo Reef, Australia	UF 21597
Pilodius areolatus	Ningaloo Reef, Australia	UF 22165
Pilodius areolatus	Scattered Islands	UF 20226
Pilodius areolatus	Vanuatu	UF 8567
Pilodius areolatus	Reunion Island	UF 12584
Pilodius areolatus	Palau	UF 3894
Pilodius areolatus	Solomon Islands	UF 2518
Pilodius areolatus	Cook Islands	UF 11716
Pilodius granulatus	Philippines	ZRC 2013.1664
Pilodius granulatus	Bali, Indonesia	NMNH BALI_1770
Pilodius granulatus	Singapore	UF 36180a
Pilodius granulatus	Singapore	UF 36195
Pilodius granulatus	Bintan, Indonesia	ZRC 1999.0379
Pilodius granulatus	Singapore	ZRC 2013.1643
Pilodius granulatus	Singapore	ZRC 1999.0287
Pilodius granulatus	Panglao, Philippines	ZRC 2013.0733
Pilodius granulatus	Panglao, Philippines	ZRC 2013.0737
Pilodius granulatus	Lizard Island, Australia	UF 17123
Pilodius granulatus	Lizard Island, Australia	UF 18203
Pilodius granulatus	Lizard Island, Australia	UF 17011
Pilodius maotieni	Guam	USNM 1188365
Pilodius maotieni	Guam	USNM 1188362
Pilodius maotieni	Lizard Island, Australia	UF 18145
Pilodius maotieni	Papua New Guinea	UF 2631
Pilodius maotieni	Philippines	ZRC 2013.1645a

Pilodius maotieni	Philippines	ZRC 2013.1646
Pilodius maotieni	Lizard Island, Australia	UF 18355
Pilodius maotieni	Bali, Indonesia	UF BALI_1663
Pilodius maotieni	Bird Island, Australia	UF 18355
Pilodius maotieni	Guam	UF 997
Pilodius maotieni	Guam	UF 1298
Pilodius maotieni	Philippines	ZRC 2013.1645b
Pilodius miersi	Heron Island, Australia	UF 24873
Pilodius miersi	Heron Island, Australia	UF 25142
Pilodius miersi	Heron Island, Australia	UF 25804
Pilodius miersi	Heron Island, Australia	UF 25930
Pilodius miersi	Heron Island, Australia	UF 25868
Pilodius miersi	Heron Island, Australia	UF 25895
Pilodius miersi	Heron Island, Australia	UF 25907
Pilodius miersi	Heron Island, Australia	UF 24734
Pilodius miersi	Heron Island, Australia	UF 24758
Pilodius miersi	Papua New Guinea	UF 3857
Pilodius miersi	Lizard Island, Australia	UF 17475
Pilodius miersi	Heron Island, Australia	UF 25805
Pilodius miersi	Panglao, Philippines	ZRC 2013.0732a
Pilodius miersi	Panglao, Philippines	ZRC 2013.0741
Pilodius moranti	Australia	QM w15143
Pilodius moranti	Australia	QM w15142b
Pilodius moranti	Australia	QM 15454
Pilodius moranti	Australia	QM 15142b
Pilodius nigrocrinitus	Heron Island, Australia	UF 25666
Pilodius nigrocrinitus	New Caledonia	UF 18008
Pilodius nigrocrinitus	Solomon Islands	UF 3331a
Pilodius nigrocrinitus	Solomon Islands	UF 3398
Pilodius nigrocrinitus	Anambas, Indonesia	ZRC 2003.0554a
Pilodius nigrocrinitus	Solomon Islands	UF 3331b
Pilodius nigrocrinitus	Great Barrier Reef	UF 17075
Pilodius nigrocrinitus	Philippines	ZRC 2013.1649a
Pilodius nigrocrinitus	Anambas, Indonesia	ZRC 2003.0554b
Pilodius nigrocrinitus	Bali, Indonesia	ZRC rBALI_0356
Pilodius nigrocrinitus	Philippines	ZRC 2013.1649b
Pilodius pilumnoides	Lizard Island, Australia	UF 17430
Pilodius pilumnoides	Palau	UF 5119
Pilodius pilumnoides	Singapore	ZRC 1989.3428a
Pilodius pilumnoides	Singapore	ZRC 1989.3428b
Pilodius pilumnoides	Singapore	ZRC 1989.3429a
Pilodius pilumnoides	Tioman, Malaysia	ZRC 1985.1506
Pilodius pilumnoides	Vanuatu	ZRC 2013.1653
Pilodius pilumnoides	Palau	USNM 1181389
Pilodius pilumnoides	Palau	UF 3852
Pilodius pilumnoides	Panglao, Philippines	ZRC 2013.1698a
Pilodius pilumnoides	Panglao, Philippines	ZRC B13

Pilodius pilumnoides	Panglao, Philippines	ZRC 2013.0734
Pilodius pilumnoides	Panglao, Philippines	ZRC 2013.1698b
Pilodius pilumnoides	Indonesia	ZRC 2013.2003.0559
Pilodius pubescens	Heron Island, Australia	UF 24669
Pilodius pubescens	Japan	ZRC 2013.1654
Pilodius pubescens	Bali, Indonesia	NMNH BALI_2269
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_1153
Pilodius pubescens	Philippines	UF 6762
Pilodius pubescens	Lizard Island, Australia	UF 17341
Pilodius pubescens	Santo	ZRC 2013.1657
Pilodius pubescens	Heron Island, Australia	UF 24814a
Pilodius pubescens	Heron Island, Australia	UF 24814b
Pilodius pubescens	Lizard Island, Australia	UF 17084
Pilodius pubescens	Lizard Island, Australia	UF 17085
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_1411
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_1304
Pilodius pubescens	Heron Island, Australia	UF 24647
Pilodius pubescens	Heron Island, Australia	UF 24969
Pilodius pubescens	Heron Island, Australia	UF 25518
Pilodius pubescens	Bali, Indonesia	NMNH BALI_1712
Pilodius pubescens	Majuro	UF 13700
Pilodius pubescens	Japan	ZRC 2013.1654
Pilodius pubescens	Solomon Islands	UF 3359
Pilodius pubescens	New Caledonia	UF 3429
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_1502
Pilodius pubescens	Philippines	ZRC 2013.1657
Pilodius pubescens	Heron Island, Australia	UF 24650
Pilodius pubescens	Heron Island, Australia	UF 24909a
Pilodius pubescens	Heron Island, Australia	UF 24909b
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_2052
Pilodius pubescens	Bali, Indonesia	NMNH BALI_2595
Pilodius pubescens	Aceh, Indonesia	NMNH ACEH_1181
Pilodius pubescens	Bali, Indonesia	NMNH BALI_2597
Pilodius pubescens	Solomon Islands	UF 2535
Pilodius pugil	Guam	UF 2814a
Pilodius pugil	Kirimati	UF 1282a
Pilodius pugil	New Caledonia	UF 37968
Pilodius pugil	Gambier Islands	UF 35494
Pilodius pugil	Mo'orea, French Polynesia	UF MOO_12185_larva
Pilodius pugil	Mo'orea, French Polynesia	UF 9877
Pilodius pugil	Mo'orea, French Polynesia	UF 18048
Pilodius pugil	Mo'orea, French Polynesia	UF MOO_12901_larva
Pilodius pugil	Mo'orea, French Polynesia	UF MOO_12311_larva
Pilodius pugil	Mo'orea, French Polynesia	UF MOO_12256_larva
Pilodius pugil	Mo'orea, French Polynesia	UF 10003
Pilodius pugil	Lizard Island, Australia	UF 17095
Pilodius pugil	New Caledonia	UF 3430

Pilodius pugil	Solomon Islands	UF 3196
Pilodius pugil	Heron Island, Australia	UF 25532
Pilodius pugil	Guam	UF 2955
Pilodius pugil	Kirimati	UF 1282b
Pilodius pugil	Reunion Island	UF 12643
Pilodius pugil	Reunion Island	UF 12850
Pilodius pugil	Reunion Island	UF 12558
Pilodius pugil	Majuro	UF 29675
Pilodius pugil	Guam	UF 2839
Pilodius scabriculus	Tuamotu Islands	UF 1595
Pilodius scabriculus	Tuamotu Islands	UF 1614
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_0418
Pilodius scabriculus	Guam	UF 15071
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL493A
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL505
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL508
Pilodius scabriculus	Cook Islands Islands	UF 11714
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL501
Pilodius scabriculus	Cook Islands Islands	UF 11714
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL501
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_DL493
Pilodius scabriculus	Mo'orea, French Polynesia	UF 9890
Pilodius scabriculus	Okinawa, Japan	ZRC 2013.1662
Pilodius scabriculus	Mo'orea, French Polynesia	UF 15407
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_12186_larva
Pilodius scabriculus	Mo'orea, French Polynesia	UF MOO_12195_larva
Pilodius scabriculus	Line Islands	UF 10513
Pilodius spinipes	Madagascar	UF 14327
Pilodius spinipes	Red Sea	UF 32990
Pilodius spinipes	Madagascar	UF 14362
Pilodius spinipes	Red Sea	UF 32959a
Pilodius spinipes	Mayotte	UF 13619
Pilodius spinipes	Chagos Archipelago	ZRC 2013.0768
Pilodius spinipes	Gulf of Oman	UF 7802
Pilodius spinipes	Mayotte	UF 13571
Pilodius spinipes	Madagascar	UF 14361
Pilodius spinipes	Madagascar	UF 14359
Pilodius spinipes	Madagascar	UF 14583
Pilodius spinipes	Madagascar	UF 14029
Pilodius spinipes	Chagos Archipelago	ZRC 2013.0769
Pilodius spinipes	Red Sea	UF 32959a
Pilodius spinipes	Oman	UF 18026
Pilodius spinipes	Red Sea	UF 32990a
Soliella flava	Line Islands	UF 11005
Soliella flava	Mo'orea, French Polynesia	UF MOO_0299
Soliella flava	Hawaiian Islands	UF 12140
Soliella flava	Hawaiian Islands	UF 12153

Soliella flava	Hawaiian Islands	UF 12223
Soliella flava	French Frigate Shoals	UF 12254
Soliella flava	French Frigate Shoals	UF 12079
Soliella flava	Line Islands	UF 10524
Soliella flava	Solomon Islands	UF 3362
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Soliella flava	Line Islands	UF 10515
Soliella flava	Bali, Indonesia	ZRC rBALI_0301
Soliella flava	Bali, Indonesia	NMNH BALI_2730
Soliella flava	Mo'orea, French Polynesia	UF 23898
Soliella flava	Mo'orea, French Polynesia	UF 15457
Soliella flava	Mo'orea, French Polynesia	UF 16382
Soliella flava	Mo'orea, French Polynesia	UF 37975
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Soliella flava	Guam	USNM 1188306a
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Soliella flava	Mo'orea, French Polynesia	UF 18380
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Soliella flava	Mo'orea, French Polynesia	UF 15680
Soliella flava	Bali, Indonesia	UF BALI_1297
Soliella flava	Philippines	ZRC 2013.0727a
Soliella flava	Bali, Indonesia	NMNH BALI_2266
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Soliella flava	Mo'orea, French Polynesia	UF MOO_5161
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Soliella flava	Panglao, Philippines	ZRC 2013.1631
Soliella flava	Tuamotu Islands	UF 1642
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Soliella flava	Christmas Island	ZRC 2013.1632
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Soliella flava	Line Islands	UF 10518
Soliella flava	Bali, Indonesia	NMNH BALI_1283
Soliella flava	Mo'orea, French Polynesia	UF MOO_0313
Soliella melanospinis	Heron Island, Australia	UF 24812
Soliella melanospinis	Aceh, Indonesia	NMNH ACEH_2168
Soliella melanospinis	Ningaloo Reef, Australia	ZRC 2013.1639
Soliella melanospinis	Bali, Indonesia	NMNH BALI_1128
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Soliella melanospinis	Chagos Archipelago	ZRC 2013.0782a

Soliella melanospinis	Philippines	ZRC 2013.1647
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Soliella melanospinis	Scattered Islands	UF 20595
Soliella melanospinis	Bali, Indonesia	NMNH BALI_1862
Soliella melanospinis	Ningaloo Reef, Australia	UF 22414
Soliella melanospinis	Heron Island, Australia	UF 25004
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Soliella melanospinis	Bali, Indonesia	NMNH BALI_1621
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Soliella melanospinis	Bali, Indonesia	NMNH BALI_2921
Soliella melanospinis	Reunion Island	UF 12825
Soliella melanospinis	Solomon Islands	UF 2544
Soliella melanospinis	Bali, Indonesia	NMNH BALI_2570
Soliella melanospinis	Bali, Indonesia	NMNH BALI_1869
Soliella melanospinis	Palau	UF 3902
Soliella melanospinis	Bali, Indonesia	NMNH BALI_2600
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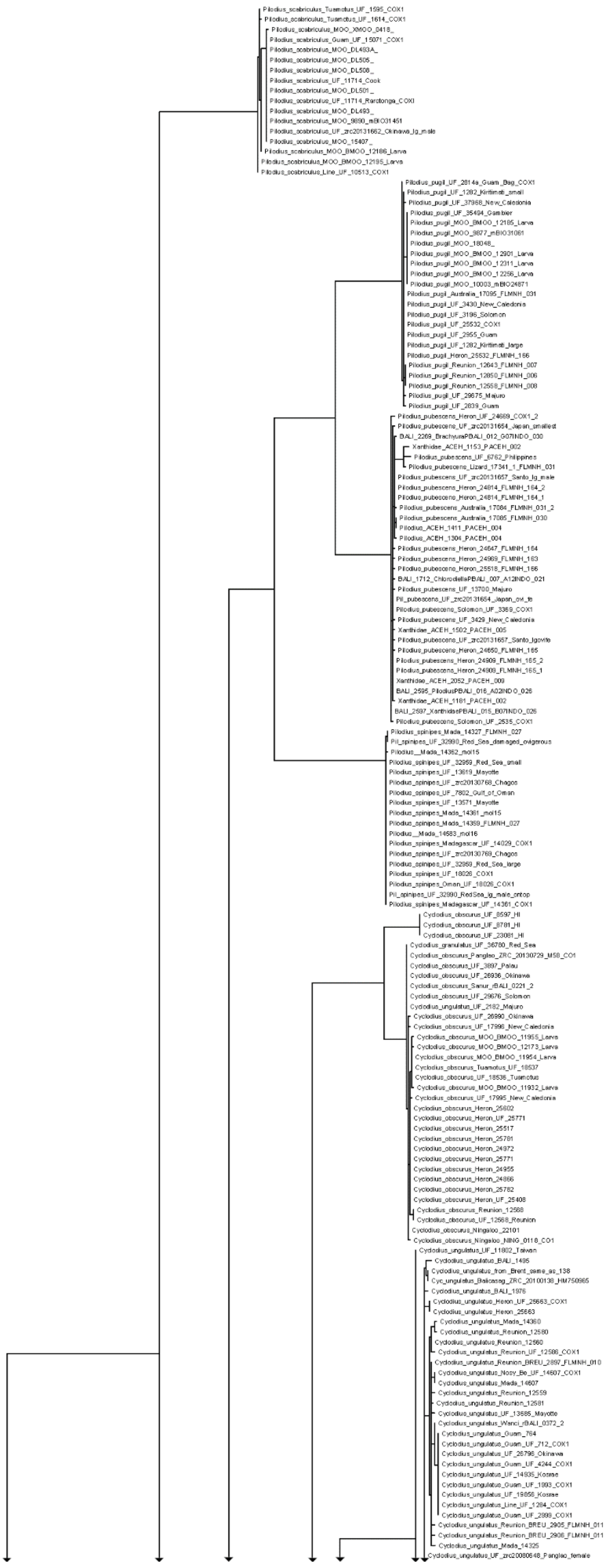
Soliella melanospinis	Ningaloo Reef, Australia	ZRC 2013.1637



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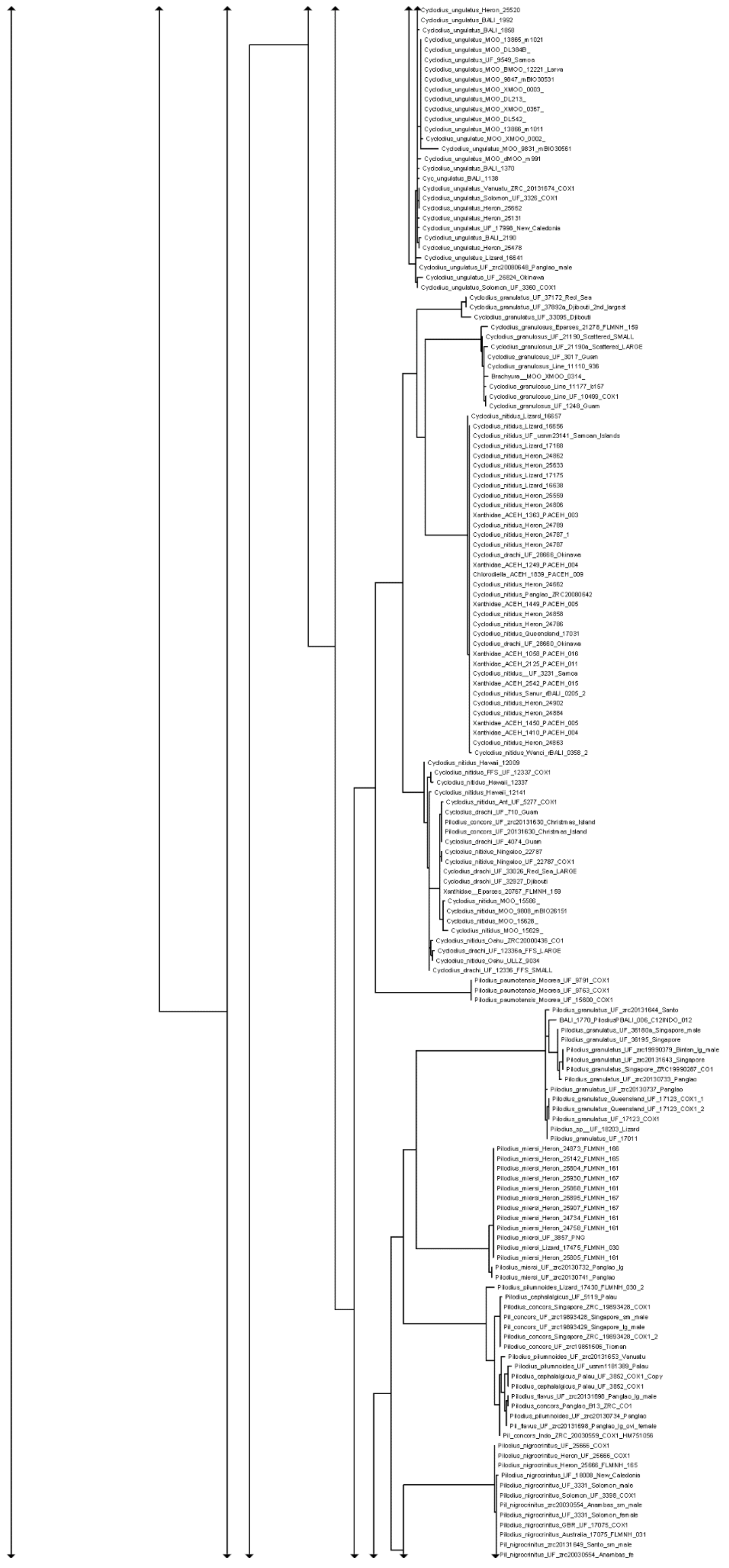
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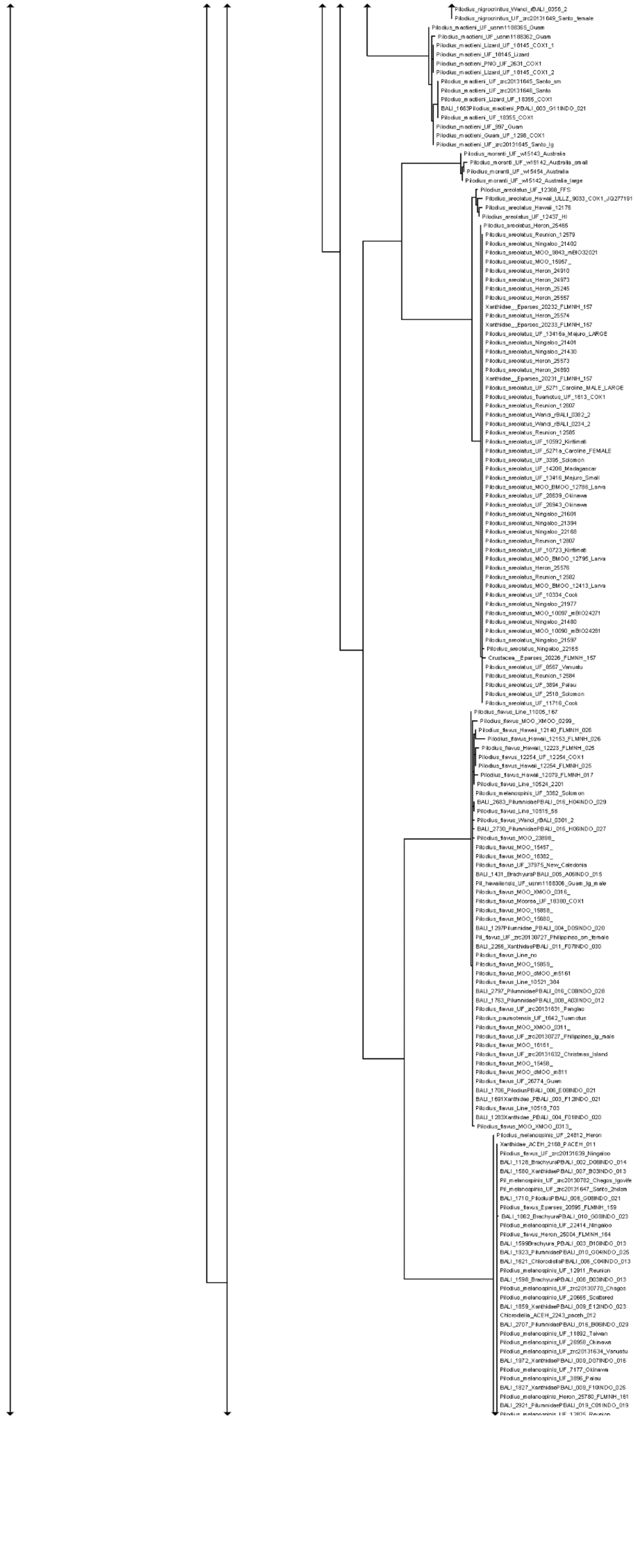

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Pilodius_maotieni_Lizard_UF_18355_COX1
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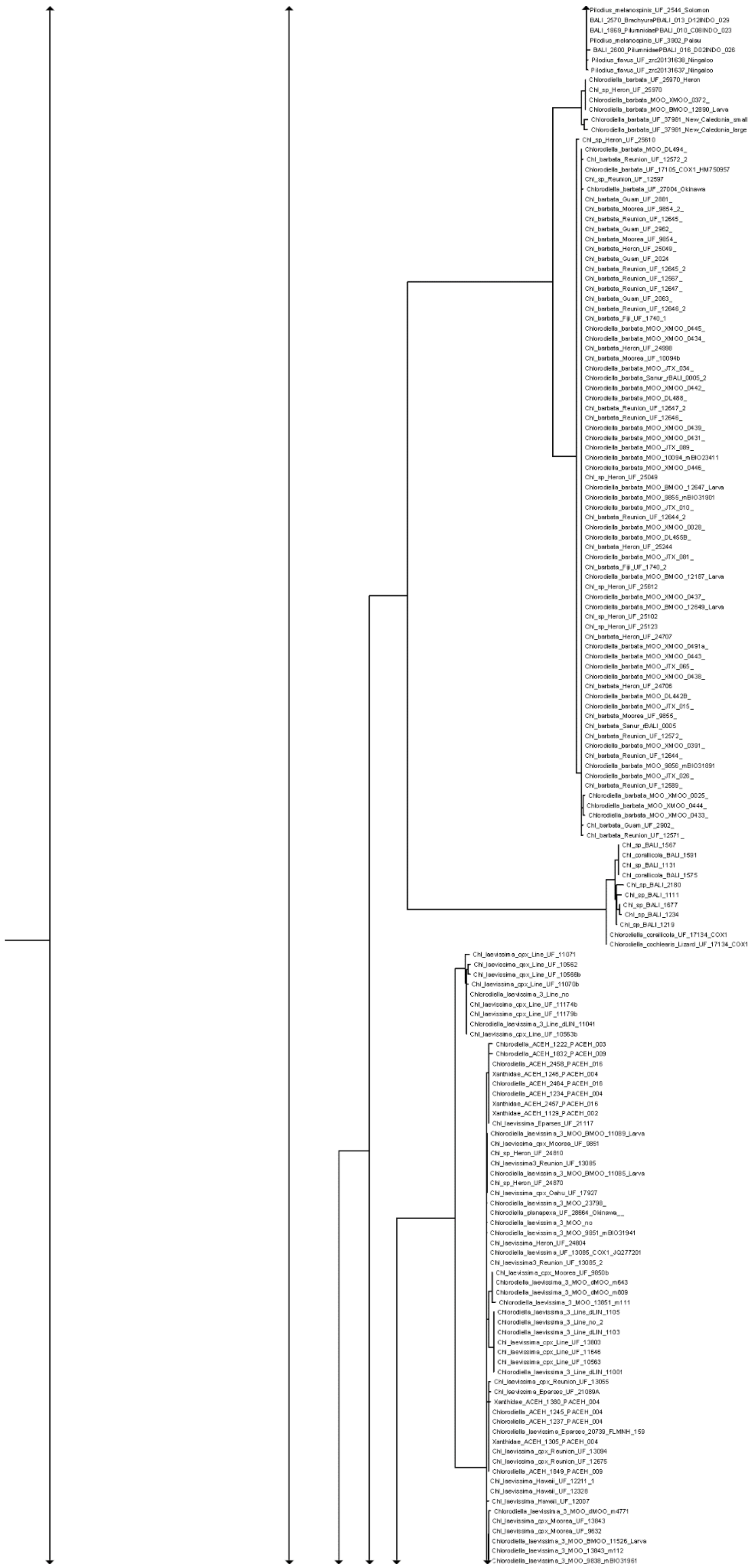

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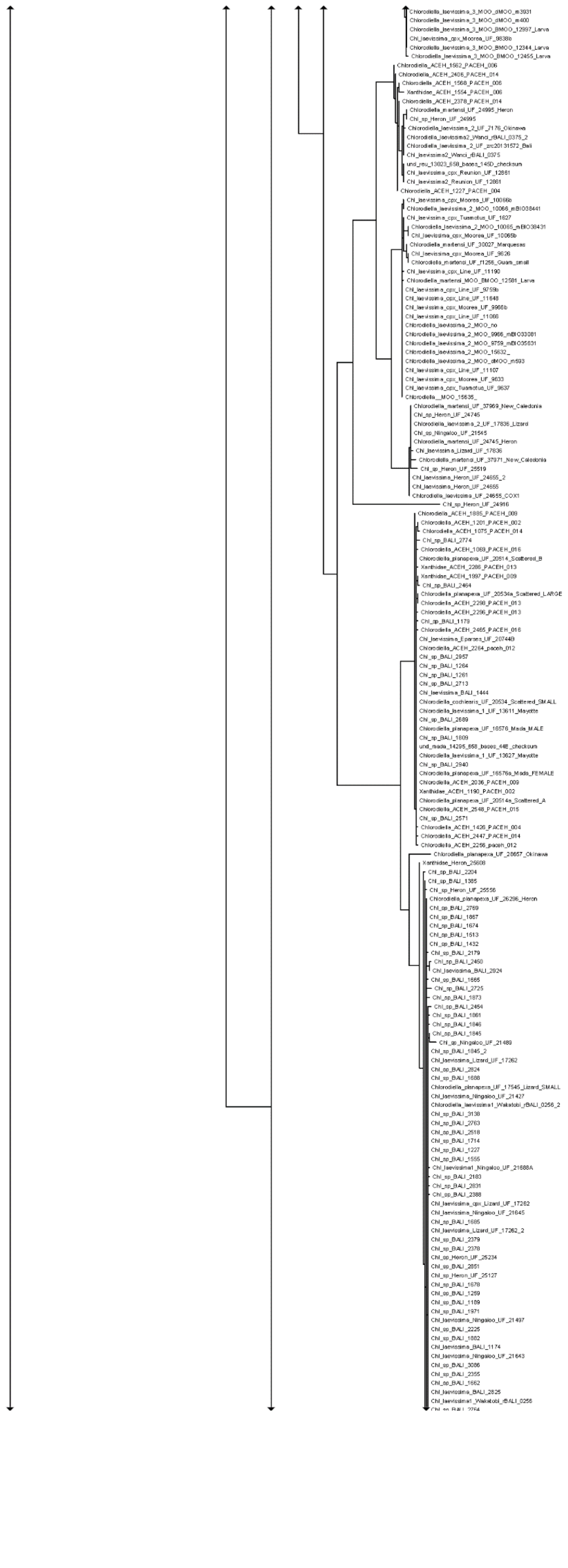
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Chlorodiella_laevissima_1_UF_13611_Mayotte
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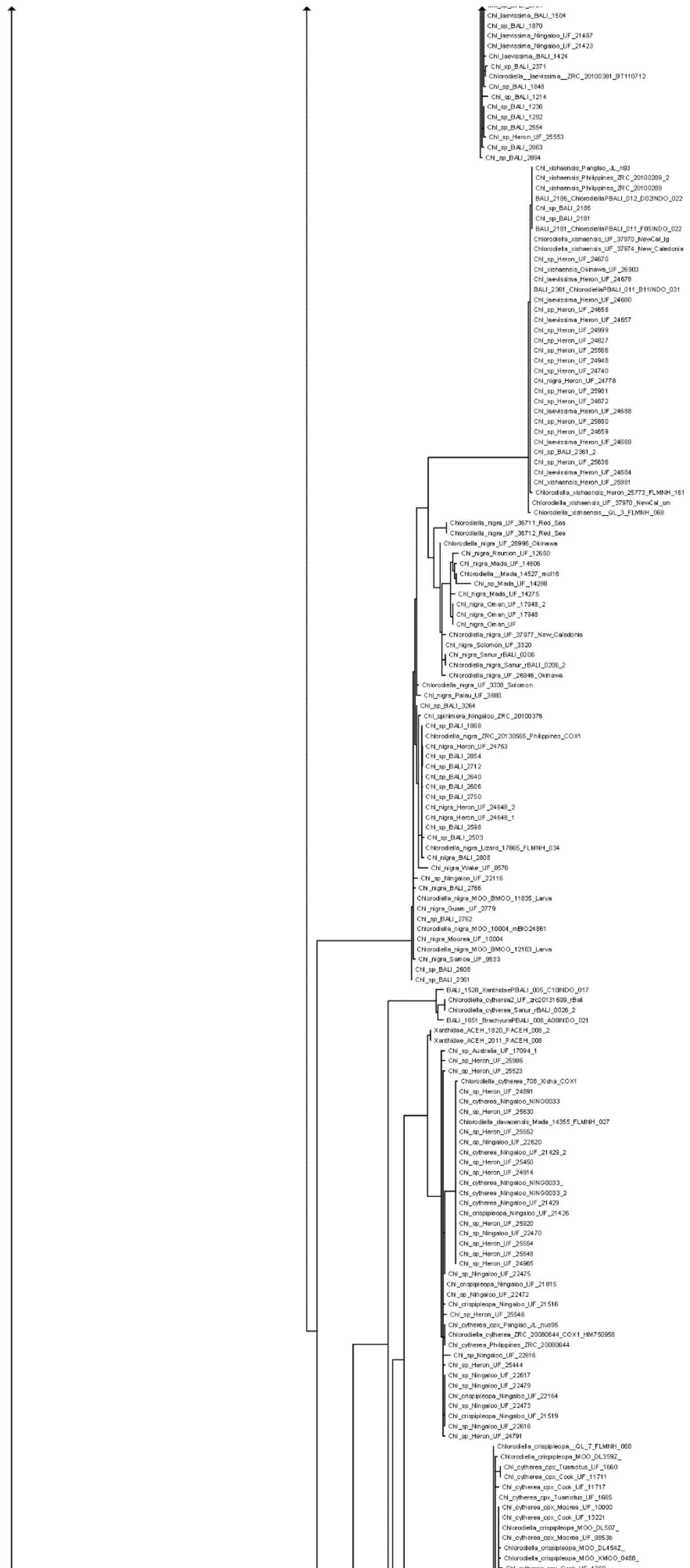
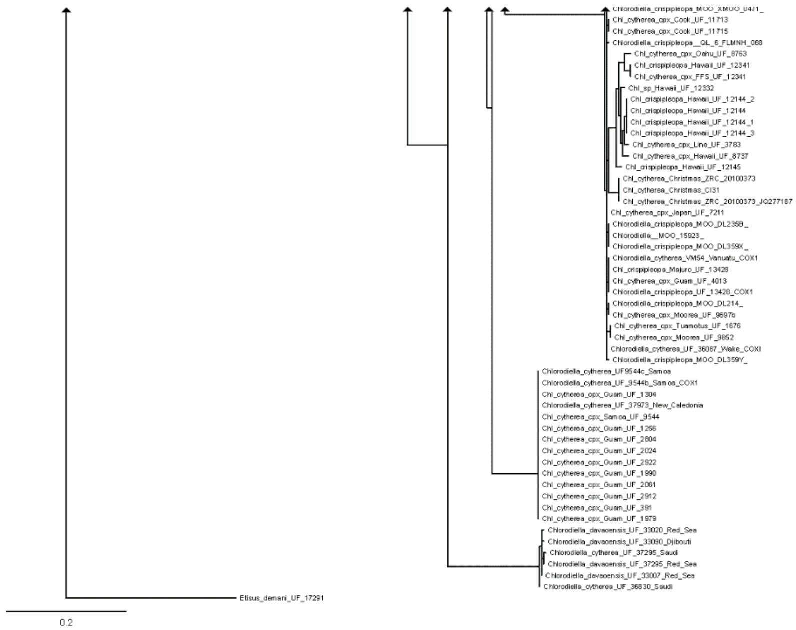
Chlorodiella_planapexa_UF_16576_Mada_MALE
Chl_sp_BALI_1809
und_mada_14295_658_bases_44E_checksum
Chlorodiella_laevissima_1_UF_13627_Mayotte
Chl_sp_BALI_2940
Chlorodiella_planapexa_UF_16576a_Mada_FEMALE
Chlorodiella_ACEH_2036_PACEH_009
Xanthidae_ACEH_1190_PACEH_002
Chlorodiella_planapexa_UF_20514a_Scattered_A
Chlorodiella_ACEH_2548_PACEH_015
Chl_sp_BALI_2571
Chlorodiella_ACEH_1426_PACEH_004
Chlorodiella_ACEH_2447_PACEH_014
Chlorodiella_ACEH_2256_paceh_012
Chlorodiella_planapexa_UF_28657_Okinawa
Xanthidae_Heron_25608
Chl_sp_BALI_2204
Chl_sp_BALI_1385
Chl_sp_Heron_UF_25556
Chlorodiella_planapexa_UF_26296_Heron
Chl_sp_BALI_2769
Chl_sp_BALI_1867
Chl_sp_BALI_1674
Chl_sp_BALI_1513
Chl_sp_BALI_1432
Chl_sp_BALI_2179
Chl_sp_BALI_2450
Chl_laevissima_BALI_2924
Chl_sp_BALI_1665
Chl_sp_BALI_2725
Chl_sp_BALI_1873
Chl_sp_BALI_2454
Chl_sp_BALI_1861
Chl_sp_BALI_1846
Chl_sp_BALI_1845
Chl_sp_Ningaloo_UF_21489
Chl_sp_BALI_1845_2
Chl_laevissima_Lizard_UF_17262
Chl_sp_BALI_2824
Chl_sp_BALI_1688
Chlorodiella_planapexa_UF_17545_Lizard_SMALL
Chl_laevissima_Ningaloo_UF_21427
Chlorodiella_laevissima1_Wakatobi_rBALI_0256_2
Chl_sp_BALI_3138
Chl_sp_BALI_2763
Chl_sp_BALI_2518
Chl_sp_BALI_1714
Chl_sp_BALI_1227
Chl_sp_BALI_1555
Chl_laevissima1_Ningaloo_UF_21688A
Chl_sp_BALI_2183
Chl_sp_BALI_2831
Chl_sp_BALI_2388
Chl_laevissima_cpx_Lizard_UF_17262
Chl_laevissima_Ningaloo_UF_21645
Chl_sp_BALI_1685
Chl_laevissima_Lizard_UF_17262_2
Chl_sp_BALI_2379
Chl_sp_BALI_2378
Chl_sp_Heron_UF_25234
Chl_sp_BALI_2851
Chl_sp_Heron_UF_25127
Chl_sp_BALI_1678
Chl_sp_BALI_1259
Chl_sp_BALI_1189
Chl_sp_BALI_1971
Chl_laevissima_Ningaloo_UF_21497
Chl_sp_BALI_2225
Chl_sp_BALI_1882
Chl_laevissima_BALI_1174
Chl_laevissima_Ningaloo_UF_21643
Chl_sp_BALI_3086
Chl_sp_BALI_2355
Chl_sp_BALI_1662
Chl_laevissima_BALI_2825
Chl_laevissima1_Wakatobi_rBALI_0256





SM 5. COXI genetree of the Chlorodiellinae showing specimens, localities and catalog numbers.

SM 6. List of terminal taxa generated for this study with locality, catalogue and GenBank accession number

Taxa	Locality	Catalog number	GenBank accession number			
			12S	16S	COXI	H3
Chlorodiella barbata (Borradaile, 1900)	New Caledonia	UF 37981	KJ938463	KM888870	KP163568	KP163617
Chlorodiella corallicola Miyake & Takeda, 1968	Lizard Island	UF 17134	KJ938482	KM888862	KP163569	KP163619
Chlorodiella cytherea (Dana, 1852)	Marshall Islands	UF 13428	KJ938489	KM888852	KP163577	KP163621
Chlorodiella nigra (Forskål, 1775)	New Caledonia	UF 37977	KJ938456	KM888873	KP163579	KP163625
Chlorodiella xishaensis Chen & Lan, 1978	Heron Island	UF 25981	KJ938464	KM888841	KP163578	KP163626
Cyclodius granulatus (Targioni-Tozzetti, 1877)	Red Sea	UF 37172	KJ938469	KM888865	KP163588	KP163631
Cyclodius granulosus De Man, 1888	Palmyra Atoll	UF 10499	KJ938465	KM888866	KP163589	KP163630
Cyclodius nitidus (Dana, 1852)*	Okinawa	UF 28660	KJ938474	KM888844	KP163590	KP163632
Cyclodius obscurus (Hombron & Jacquinot, 1846)	Hawaiian Islands	UF 23081	KJ938481	KM888847	KP163603	KP163633
Cyclodius ungulatus (H. Milne Edwards, 1834)	Reunion Island	UF 12586	KJ938467	KM888843	KP163583	KP163634
Etisus albus (Ward, 1934)	Kiribati	UF 10541	KJ938470	KM888845	KP163597	N/A
Etisus anaglyptus H. Milne Edwards, 1834	Moorea	UF 16186	KJ938468	KM888869	KP163571	KP163620
Etisus bifrontalis (Edmondson, 1935)	Hawaiian Islands	UF 12311	KJ938488	KM888842	KP163600	KP163610
Etisus bifrontalis (Edmondson, 1935)	Ningaloo Reef	UF 22204	KJ938457	KM888851	KP163601	KP163609
Etisus demani Odhner, 1925	Lizard Island	UF 17291	KJ938452	KM888875	KP163598	KP163608
Etisus frontalis (Dana, 1852)	Moorea	UF 16460	KJ938453	KM888856	N/A	KP163614
Etisus laevimanus Randall, 1840	Hawaiian Islands	UF 8783	N/A	KM888846	KP163570	N/A
Etisus sakaii Takeda & Miyake, 1968	Lizard Island	UF 16901	KJ938484	N/A	KP163567	KP163611
Etisus sakaii Takeda & Miyake, 1968	Solomon Islands	UF 3414	KJ938478	KM888849	N/A	KP163612
Kraussia rugulosa (Krauss, 1843)	Guam	UF 26571	KJ938461	KM888850	KP163599	KP163618
Liocarpilodes armiger (Nobili, 1905)	Lizard Island	UF 17268	KJ938459	KM888874	KP163573	KP163607
Liocarpilodes harmsi (Balss, 1934)	Reunion Island	UF 14819	KJ938483	KM888853	N/A	KP163605

Liocarpilodes integerrimus (Dana, 1852)	Reunion Island	UF 12674	KJ938479	KM888861	KP163602	KP163604
Liocarpilodes pacificus Balss, 1938	Heron Island	UF 24836	KJ938485	KM888871	KP163574	KP163606
Pilodius areolatus (H. Milne Edwards, 1834)	Hawaiian Islands	UF 12176	KJ938476	KM888837	KP163585	KP163613
Pilodius flavus Rathbun, 1894	Hawaiian Islands	UF 12254	KJ938480	KM888872	KP163580	KP163636
Pilodius granulatus Stimpson, 1858	Lizard Island	UF 17011	KJ938466	KM888840	KP163587	KP163637
Pilodius maotieni Serène, 1971	Lizard Island	UF 18145	KJ938477	KM888857	KP163591	KP163638
Pilodius melanospinis (Rathbun, 1911)	Heron Island	UF 25780	KJ938460	KM888838	KP163581	KP163635
Pilodius miersi (Ward, 1936)	Heron Island	UF 25804	KJ938487	KM888855	KP163592	KP163629
Pilodius moranti Clark & Galil, 1993	Coral Sea	w15454	KJ938462	KM888858	KP163584	KP163627
Pilodius nigrocrinitus Stimpson, 1859	Lizard Island	UF 17075	KJ938454	KM888868	KP163582	KP163639
Pilodius paumotensis Rathbun, 1907	Moorea	UF 15600	KJ938473	KM888864	KP163586	KP163628
Pilodius pilumnoides (White, 1848)	Palau	UF 3852	KJ938458	KM888863	KP163593	KP163640
Pilodius pubescens Dana, 1852	Heron Island	UF 24669	KJ938471	KM888860	KP163596	KP163624
Pilodius pugil Dana, 1852	Reunion Island	UF 12850	KJ938486	KM888859	KP163595	KP163623
Pilodius scabriculus Dana, 1852	Kiribati	UF 10513	KJ938475	KM888839	KP163576	KP163616
Pilodius spinipes Heller, 1861	Madagascar	UF 14029	KJ938455	KM888867	KP163594	KP163622
Tweedieia laysani (Rathbun, 1906)	Wake Island	UF 8564	KJ938472	KM888848	KP163572	KP163615
Vellodius etisoides (Takeda & Miyake, 1968)	Vanuatu	ZRC 2013.1701	N/A	KM888854	KP163575	N/A